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BONE DIGESTION AND INTESTINAL MORPHOLOGY OF THE BEARDED VULTURE

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ABSTRACT.—The diet of the bearded vulture (*Gypaetus barbatus*) consists largely of bone. Two experimental birds fed a diet of sheep ribs had a mean digestive efficiency of 50%, with most of the food being digested within 24 hr. The digestive tract of bearded vultures is not unusually long for a scavenging bird of its size, and does not contain a region for mechanical breakdown of the food. The stomach contains a high concentration of acid-secreting cells, and experiments with bone fragments in acid solutions suggested that this is the chief mechanism for decalcification. A bone diet may have a higher caloric content than an equivalent weight of soft tissues. The ecological consequences of this unusual diet are that this species is able to survive in areas with a very low availability of carcasses.

KEY WORDS: *bearded vulture; bone digestion; Gypaetus barbatus; intestinal morphology.*

Digestión de huesos y morfología intestinal de *Gypaetus barbatus*

RESUMEN.—La dieta de *Gypaetus barbatus* consiste esencialmente de huesos. Dos individuos experimentales se sometieron a una dieta de huesos de oveja, con un promedio de eficiencia digestiva del 50%, donde la mayoría del alimento llegó a digerirse en 24 h. El tracto digestivo de *G. barbatus* no es inusualmente largo para un carroñero de su tamaño y no contiene una región para la trituración mecánica del alimento. El estómago contiene una alta concentración de células secretoras de ácido, y experimentos con fragmentos en soluciones ácidas sugieren que este es el principal mecanismo para la descalsificación. Una dieta de huesos puede tener un mayor contenido calórico que un peso equivalente de tejidos blandos. Las consecuencias ecológicas de esta dieta inusual, serían que esta especie podría sobrevivir en áreas con muy baja disponibilidad de carroña.

[Traducción de Ivan Lazo]

The bearded vulture (*Gypaetus barbatus*) is a scavenger on the carcasses of large mammals in mountain regions in Africa, Asia, and Europe. It is unusual in that it eats bones. Small bones are swallowed whole and larger ones are dropped repeatedly onto rock slabs to break them into small enough fragments to be swallowed (Huxley and Nicholson 1963, Brown 1988). Several studies recently have shown that bone is not just an occasional food item, but the predominant food of the bearded vulture. Bone forms 70–90% of all food items (Hiraldo et al. 1979, Cramp and Simmons 1980, Brown and Plug 1990). Even owl pellets are eaten for their bone content (Heredia et al. 1990). Brown and

Plug (1990) showed that if wild bearded vultures were presented with a choice of bone items and meat, they would select the bone, and old, dried bones significantly more frequently than fresh bones. Some mammalian carnivores, notably the spotted hyena (*Crocuta crocuta*), can also digest bone, but this forms only a small proportion of their normal diet (Kruuk 1972). The bearded vulture is the only vertebrate known to have a diet consisting largely of bone. We present here preliminary results from feeding trials to determine the digestive efficiency of bearded vultures on this unusual diet, and the time they required for digestion. We also carried out postmortem examinations to consider whether the

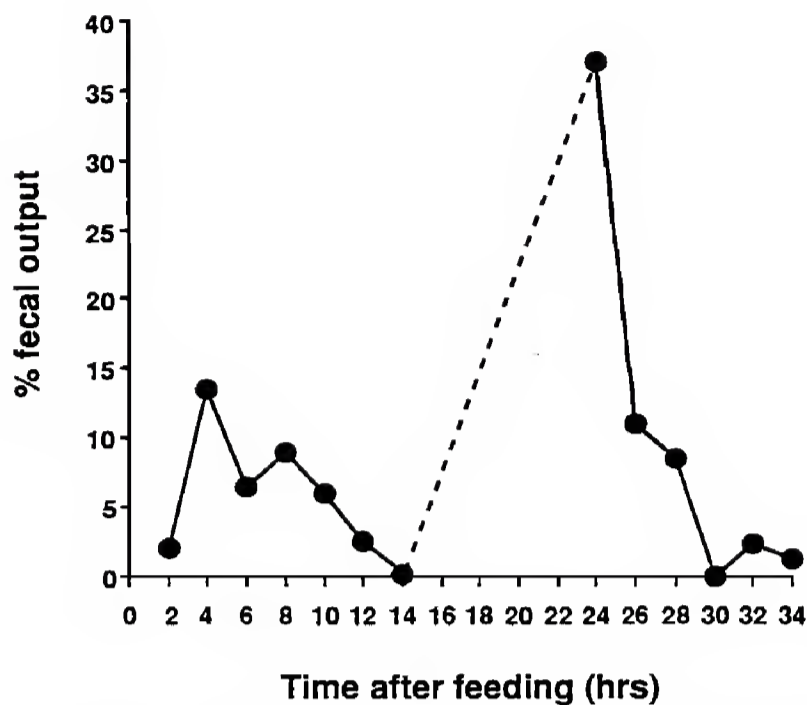


Figure 1. The time of fecal production from a pair of bearded vultures after ingestion of a bone meal.

intestine of the bearded vulture showed any specializations, and finally we speculate on the ecological implications of their diet.

METHODS

Feeding trials were carried out on two adult bearded vultures housed in the Research Zoo of Tel Aviv University, Israel in September 1992. It was not possible to separate the pair; all results presented here are mean values for the two. The cage floor was lined with sheeting to allow total fecal collection. A weighed quantity of 4-cm lengths of sheep rib bones was provided each afternoon and removed the following morning. A control sample of bone was also left outside the cage, to correct for dehydration of the bone samples left in the cage. All uneaten bone fragments were weighed and corrected for water loss to determine wet weight of bone eaten. A sample of the bone diet was dried at 70°C to constant weight to determine mean water content. This figure was used to calculate dry food intake. Bone samples were then ashed in a furnace at 535°C and ash weight used to determine mineral content of the diet. Organic content was derived from weight loss during ashing. All feces were collected daily, separated from uric acid material, and dried to constant weight at 70°C. Percent digestive efficiency was calculated as $1 - \text{total dry weight feces} / \text{total dry weight bone eaten} \times 100$. Four feeding trials were conducted over 13 d. Birds were deprived of food for 24 hr before the start of each trial.

The digestion time for food was recorded by starving the birds for 48 hr, providing them with food at 0630 H, and removing all uneaten food after they had finished feeding. The birds were then observed continuously and the time of all fecal production noted. Feces were collected and dried at 70°C. Birds were not fed again until 24 hr after the last appearance of fecal material. For security reasons, fecal collections could not be made at night.

The form in which calcium was present in the feces was investigated using X-ray diffraction analysis using Fe-filtered

Co k radiation at scanning speed 2 θ min and range 4–64 2 θ . The effects of pH and time on the rate of bone decalcification was investigated. Pieces of sheep rib bone from mature animals, as used in the feeding trials, were placed in hydrochloric acid solutions, buffered with N sodium acetate (Hale 1953), at pH 0.8, 1.1, and 1.5. The pHs used were within the range of acidity recorded from the stomachs of other raptor species (Herpol 1967, Duke et al. 1975). Solutions were maintained at 40°C in a water bath. The pH was checked every few hours and the solution replaced if necessary. The weighed bone pieces were each placed in individual vials and maintained there for 6, 12, 24, or 48 hr, after which time excess liquid was removed with paper towelling. Bone pieces were then reweighed, dried to constant weight at 70°C, and ashed in a furnace at 525°C for 24 hr. Five bone samples were used for each of the experimental treatments. We also simulated the digestive effect of combined acid and pepsin, using commercial porcine pepsin solutions in the same range of pH conditions and the time periods outlined above.

The intestinal morphology of two bearded vultures was examined in postmortem examinations. The birds died in captivity, and had been part of the breeding program for the reintroduction of bearded vultures into the Alps (Frey and Walter 1989). Samples of alimentary tract were prepared for histological examination with Mallory, haematoxylin/eosin, and periodic acid-Schiff/alcean blue stains (Gurr 1962).

RESULTS

The rib bones used in the feeding trials and the decalcification study had a mean water content of $32\% \pm 1.8$ (SE, $N = 12$), and dry bone weight was composed of $54\% \pm 1.7$ (SE) mineral content and $46\% \pm 1.7$ (SE) organic content. The mean digestive efficiency, as measured from total collection of fecal material, was $49.8\% \pm 1.3$ (SE). The digestion time for food could, unfortunately, only be measured on one occasion, when the birds ate 146 g of bone. Most fecal production occurred within 24 hr after feeding (Fig. 1). Unfortunately, it was not possible to be with the birds overnight to record when the peak fecal production occurred. Virtually all fecal material was ejected within a few hours of dawn, because fecal material was not dehydrated when collected at 0600 H. Dehydration would have occurred in the dry air conditions in Tel Aviv if feces had been produced early in the night.

The dimensions of the digestive tract of the two birds were: esophagus lengths 25 and 21 cm; stomach lengths were both 17 cm, stomach widths 6 and 5 cm; small intestine lengths (including duodenum) 184 and 185 cm; wet weight of stomachs (empty) 80 and 75 g; and wet weights of small intestines (empty) 40 and 47 g.

The length of the small intestine of the bearded vulture is shown in Fig. 2 in relation to its body size and in comparison with a range of other raptor species (for method of scaling for body size see Barton and

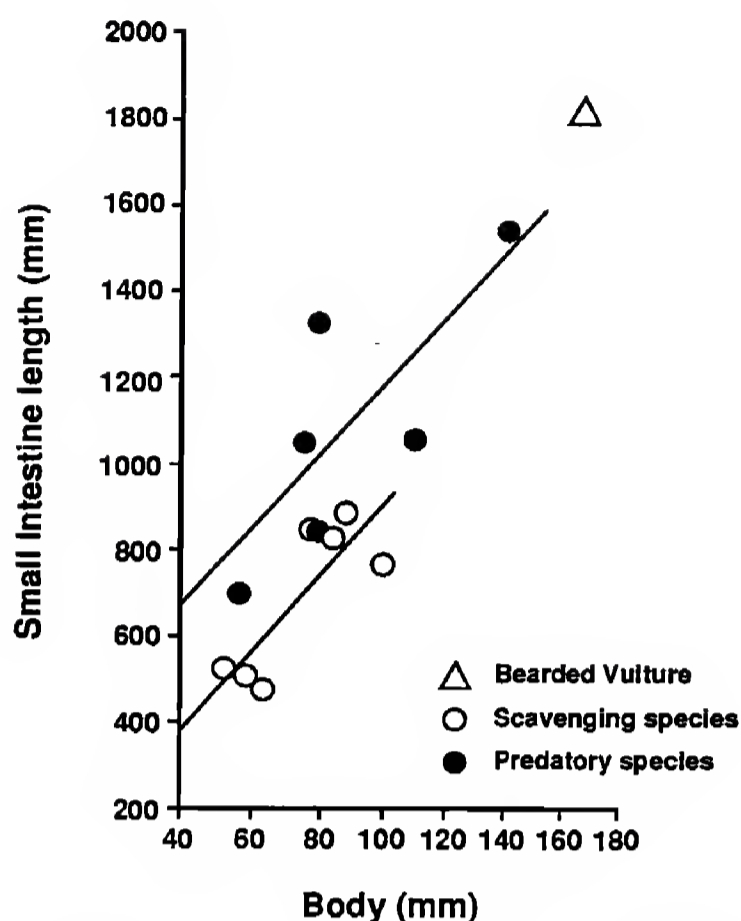


Figure 2. A comparison of the length of the small intestine of the bearded vulture in relation to an index of body size (sternum length \times sternum diagonal)^{1/2}, with data from other birds of prey which have a scavenging diet and an active chase form of predation (from Barton and Houston 1994).

Houston 1994); the intestinal length is close to that predicted for a scavenging raptor.

The digestive tract showed some specialization. The esophagus was highly elastic and expandable to allow the passage of large food items, but no clearly defined crop (a diverticulum off the esophagus) was present. The bearded vulture is the only species of vulture to lack this large storage region in front of the stomach. Irregularly shaped fragments of bone would be difficult to store in a crop and then later retrieve for passage to the stomach. Bearded vultures must use the esophagus to store food; Brown (1988) recorded birds swallowing bones at least 250 mm long and 35 mm wide, which would be too large to contain in the stomach. Bearded vultures are also occasionally seen flying with the end of a bone still projecting from the mouth.

The esophagus had a mean wall thickness of 1.3 ± 0.1 mm (SE, $N = 20$), contained no mucus glands (as is typical of vertebrates), but did have a thickened epithelial layer from 23–126 μ m thick with some keratinization underlaid by a connective tissue layer from 23–207 μ m thick. These layers, together with the elasticity of the esophagus, must provide some protection from sharp bone pieces. The gastric stomach contained

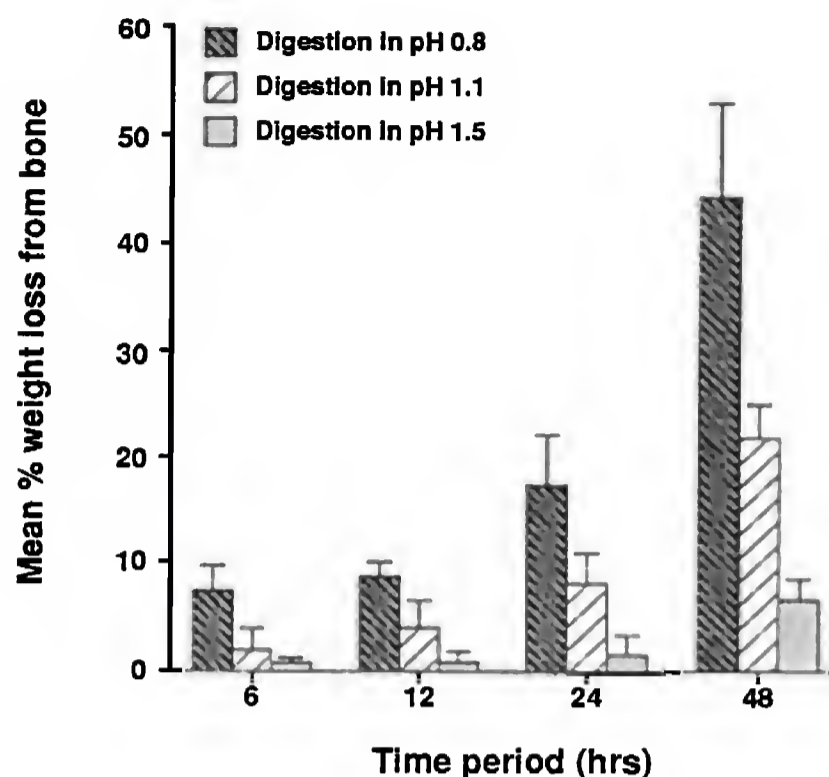


Figure 3. Weight loss of bone samples with time in solutions of different acidity.

a very high density of acid secreting cells ($\bar{x} = 109 \pm 4$ (SE) cells per 10 000 μ m², $N = 8$), with no pepsin-secreting cells visible in any of the sections we examined. Neither the gastric nor the pyloric stomach regions were highly muscular, the whole stomach wall having a mean thickness of only 2.3 ± 0.1 mm (SE, $N = 20$). There was no gizzard-like portion of the stomach which could act to mechanically grind food.

Fig. 3 shows bone weight loss in acid solutions. Both the acidity and time influence weight loss (two-way ANOVA $F = 124.9$, $df = 2,48$ and $F = 124.5$, $df = 3,48$, $P < 0.01$; Fig. 3). There was a significant interaction between the effects of time and pH, so the rate of weight loss is dependent on the acidity of the solution ($F = 21.7$, $df = 6,48$, $P < 0.01$). Loss in weight was entirely caused by demineralization, and there was no significant loss in organic content of the bone (Fig. 4). Bone fragments placed in acid solutions containing porcine pepsin solutions to simulate stomach conditions failed to show any enhanced rate of weight loss over acid solutions alone.

Analysis of feces by X-ray diffraction showed a peak profile characteristic of calcium hydroxyapatite. No other calcium salt was represented except some calcite which, together with quartz, may have been ingested as soil particles.

DISCUSSION

The diet of the bearded vulture must be among the most unusual of all birds. It is remarkable that the

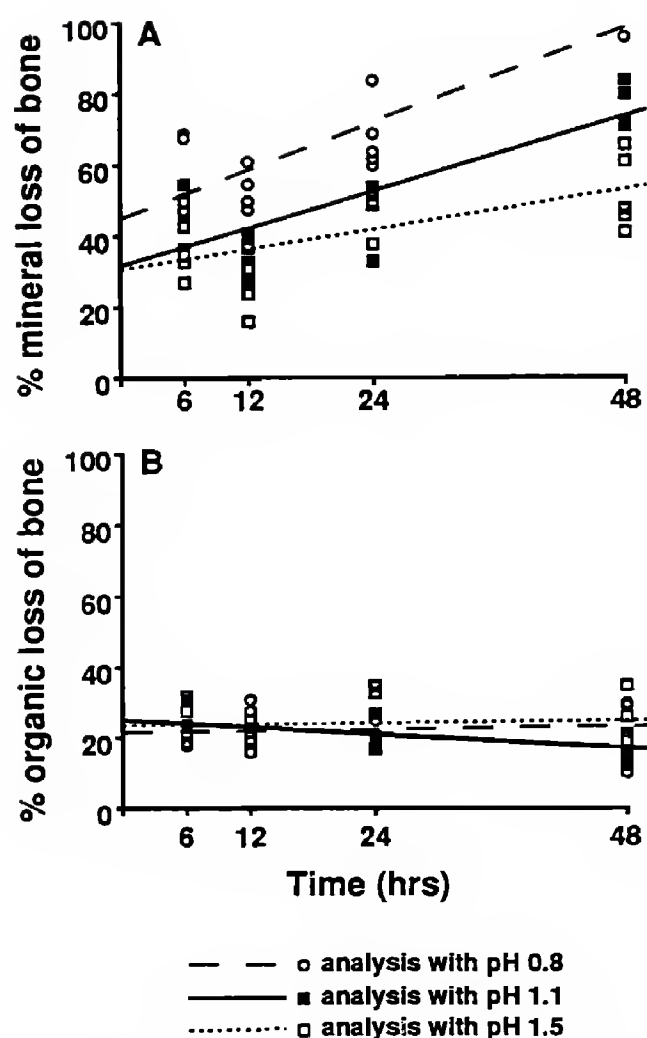


Figure 4. The effects of the level of acidity on the demineralization and loss of organic content of bone with time.

energy requirements can be derived largely from bone, but digestive efficiency on this diet is surprisingly high. Most predatory birds have digestive efficiencies between 75 and 80% (Duke et al. 1975, Barton and Houston 1993a). Bone is a complex, composite tissue with about two-thirds of the mass and one-half of its volume composed of inorganic salts. These are predominantly crystals of calcium phosphorus apatite [$\text{Ca}_3(\text{PO}_4)_2 \cdot \text{CaCO}_3$], present as tiny crystals about 40 nm long in an organic matrix which is composed of 90–96% collagen fibrils (Alexander 1983). There is also a variable amount of fat in the bone marrow. The rib bone diet used here had a mineral content of 54.2%, and the digestive efficiency of 50% is high. These figures imply that once the bone has been demineralized, the efficiency of absorption of the organic component must be almost complete. Efficiency of absorption may be assisted by the slow throughput time, for digestive efficiency increases with a reduced rate of food passage through the alimentary tract (Robbins 1983). The slow rate of digestion is almost certainly imposed by the time required to demineralize the food. Barton and Houston (1993b) gave throughput times for seven spe-

cies of birds of prey taking conventional meat diets. All seven had peak fecal output from 3–6 hr after ingestion. Bearded vultures also have some fecal production about 4 hr after feeding (Fig. 1), which may result from the small amounts of soft tissue adhering to the bones, but the bulk of fecal production is derived from bone tissue digestion and this occurs nearer to 24 hr after feeding.

Bone is such an unusual diet that the bearded vulture might be expected to have developed an unusually long digestive tract. Barton and Houston (1994) found considerable variation in small intestine length among species of predatory birds; these differences may be associated with predatory behavior. Species with active chasing methods of predation, such as falcons, seem to have comparatively short small intestines and digest their food comparatively poorly. Species which rely more on soaring flight and which do not require a high-speed chase to capture prey, such as scavengers and buzzards, have longer intestines and digest their food more efficiently (Barton and Houston 1993a). The reduced weight of a short digestive tract presumably enhances prey capture in active predators and this compensates for the reduced digestive efficiency of the smaller gut. However, Fig. 2 showed that the gut length in bearded vultures was not abnormal for a scavenging raptor.

The process by which bearded vultures break down bone tissue is not fully known. However, the esophagus and stomach show no specializations to suggest that mechanical breakdown is important. The results presented here confirm the findings of Duke et al. (1975) that the level of acidity is an important factor in the demineralization of bone. The pH levels in the bearded vulture stomach are unknown, but Houston and Cooper (1975) recorded a pH of 1 in an African white-backed vulture (*Gyps africanus*), and other raptors have been recorded with gastric pH as low as 0.7 (Herpol 1967). The stomach wall in the bearded vulture contains a high density of acid-secreting cells, and must be capable of producing a highly acidic environment. The feces of bearded vultures contained calcium hydroxyapatite, the same form of calcium as in bone. Therefore, the mineral salts seem to be leached from the bone tissue without chemical transformation. We only have one observation on the time taken for digestion, but this suggested that bearded vultures complete digestion within about 30 hr. An acid solution of pH 0.8 alone would not have completed demineralization within this time, but bone probably breaks down in the stomach much faster than in our acid solutions

because of two factors. Firstly, there will be mechanical agitation from contractions of the stomach walls. Jackson et al. (1987) showed that even gentle movement of food samples resulted in significantly greater breakdown than stationary conditions. Bone fragments became comparatively soft after a period in strong acid, and gentle grinding together would have substantially increased their rate of breakdown. Secondly, the action of the acid will be augmented by pepsin activity to break down the collagen matrix. We were not able to obtain a commercial form of pepsin which remained active in our experimental conditions. Pepsins operate over very narrow pH ranges, which vary considerably between species (Withers 1992). Presumably bearded vultures have protein-splitting enzymes that have optimum activity in highly acidic solutions.

Very little is known of calcium metabolism in raptors, but bearded vultures are obviously adapted for a diet which has a highly unusual calcium/phosphorus ratio and exceptionally high calcium levels. Recommended feeds for domestic chickens should contain no more than 1.2% calcium (Scott et al. 1982) whereas bone contains 15–18% calcium.

Brown (1988) showed that mammal bones have a higher energy content than muscle tissue (6.7 and 5.8 KJ/g respectively) partly because of their high fat content. Brown and Plug (1990) calculated that a bearded vulture taking a diet of 70% bone, 25% muscle, and 5% skin (the best estimate available of natural diet) would ingest 674 KJ energy per 100 g, compared to 586 KJ energy for an equivalent weight of muscle. We have shown the digestive efficiency of bone to be 50%, and if we assume 75% efficiency for soft tissues, then for each 100 g of bone-dominated diet the bird would absorb 387 KJ compared to 440 KJ on a pure muscle diet. A bone-based diet is therefore energetically almost as valuable as a meat-based diet. A bone-based diet, however, has one major advantage in that it does not decompose. A skeleton left on a mountain hillside will rapidly dehydrate sufficiently to prevent bacterial breakdown of the mineralized tissues and the fatty marrow. Bearded vultures are known to return to skeletons after several months to continue feeding. All other scavenging birds which feed on soft tissues are faced with a race against time when they locate a carcass. If they do not consume the meat within a short period of time it will be destroyed by bacteria or insect larvae (Houston 1979). This has major implications for the availability of food for bone-eating and meat-eating scavengers. If, for example, bones remain in an edible condition for 10 times the length of time that soft tissues

remain in an edible condition, this means that a bone-scavenger can survive with only one-tenth the number of carcasses within its foraging range compared to a meat scavenger. This is probably why bearded vultures are so successful in high mountain regions, such as Tibet and the Himalayas. Such areas have extremely low ungulate biomass and few carcasses become available. But when they do a bearded vulture can rely on them for a long period of time.

If bone is such a useful diet, why do other raptors not exploit it? Bone is a heavy food which takes a comparatively long time to digest. It is notable that even bearded vultures prefer to eat old bones rather than fresh (Brown and Plug 1990), probably because they will have lost about 30% of their weight. All vultures have extremely low energy flight costs because of their dependence on soaring. Other raptors which rely on powered flight, less efficient gliding, or species living in regions with less powerful soaring conditions, might expend too much energy when flying with a stomach full of heavy bone to warrant feeding on this diet. In addition, the slow time required for digestion of bone will preclude small species from using this diet, for their higher metabolic rates require a faster delivery of energy from the digestive tract. Perhaps only a very large, soaring bird living in a mountainous habitat with powerful upcurrents could afford to specialize in this way.

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BEHAVIOR OF COLONIAL COMMON KESTRELS (*Falco tinnunculus*) DURING THE POST-FLEDGING DEPENDENCE PERIOD IN SOUTHWESTERN SPAIN

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ABSTRACT.—Common kestrel (*Falco tinnunculus*) chicks from a small breeding colony in southwestern Spain fledged an average of 31 d after hatching and remained at the colony, depending on their parents for food, an average of 16 more days. Fledglings perched close to and socialized with their siblings and unrelated fledglings. Fledglings started to use hovering flights a mean of 9.7 d after fledging. Social play, in the form of chases among fledglings, manipulative play with objects, and the capture of insects by the fledglings were observed before fledglings became independent.

KEY WORDS: *fledging; post-fledging dependence period; play; common kestrel; Falco tinnunculus.*

Comportamiento del cernícalo vulgar (*Falco tinnunculus*) durante el periodo de emancipación en suroeste de España

RESUMEN.—En una pequeña colonia de cernícalos vulgares (*Falco tinnunculus*) en el suroeste de España, los pollos volaron por primera vez una media de 31 días después de la eclosión y permanecieron en la colonia una media de 16 días más dependiendo de sus padres. Los jóvenes tenían un comportamiento social y se posaban junto a sus hermanos y junto a otros jóvenes no emparentados. Los jóvenes empezaron a cernirse una media de 9.7 días después del primer vuelo. Antes de que los jóvenes se independizaran se observaron juegos sociales, bajo la forma de persecuciones entre jóvenes, juegos de manipulación de objetos y capturas de insectos.

[Traducción Autor]

The post-fledging dependence period, defined as the period after the first flight during which young birds continue to depend on their parents for food, has received little attention in raptors. The common kestrel (*Falco tinnunculus*) is a well-studied species, and its breeding cycle has been relatively well documented (e.g., Newton 1979, Cramp and Simmons 1980, Cade 1982, Village 1990). However, information about the duration of the post-fledging dependence period and behavior of parents and offspring during this period is scarce. From casual observations, it is estimated that the young remain near the nest for at least 2–3 wk after fledging (Village 1990). Tinbergen (1940) provided some observations of the behavior of a wild brood during 20–25 d of post-fledging dependency. Komen and Myer (1989) described the behavior of nine fledglings held in captivity and released at the time of fledging. These fledglings continued to return for food for an average of 42 d. Komen and Myer (1989) estimated the duration of the post-fledging dependence period of a wild brood of three fledglings to be 37 d.

This study gives the estimated duration of post-fledging dependency in common kestrels from a small colony in southwestern Spain, and describes the adult and fledgling behavior during this part of the breeding cycle.

STUDY AREA AND METHODS

Observations were carried out in the spring and summer of 1989 in a mixed colony of common kestrel and lesser kestrel (*Falco naumanni*) in an abandoned sandstone quarry (37°29'N, 5°38'W) near Carmona, Seville, southwestern Spain. Common kestrels (12–15 pairs started breeding) nested on ledges and in holes of a cliff approximately 20 m high and 200 m long. The minimum distance between neighboring nests was 6 m. The area surrounding the quarry was a flat and open agricultural plain with small fields of cereals (wheat and barley), sunflowers, olive and fruit trees.

We banded 22 common kestrel chicks from five nests when they were 19–30 d old with laminated plastic bands with an alphanumeric code that could be read with a telescope. Brood sizes at the time of banding were three, four, four, five, and five chicks. One of the chicks had already fledged when banded and it was not known from which nest it came. At least one other nest produced two

fledglings that were not banded. Four chicks, each from a different nest, were equipped with radiotransmitters attached with a backpack harness (Beske 1978; weight with harness 9 g, 4% of body mass). The eight chicks without radiotransmitters from both of the nests with five chicks, were marked with a 2.5 cm strip of colored SAF-LAG pierced on the upper part of the wing (Young and Kochert 1987), which allowed individual recognition also in flight. Adult common kestrels were not marked, and they could not be identified once they started feeding the fledglings out of the nest.

Observations were performed by one observer from a variable point 130 m from the cliff, with 10× binoculars and a 60–80× field scope. The whole colony was observed for approximately 4-hr periods, between 0630–2000 GMT, every 1–3 d (47 hr in 13 d). Observations started 17 June, when some of the chicks were starting to fledge, and ended 14 July when all but five banded kestrels (one radiotagged) had left the vicinity of the colony. Fledglings still at the colony on the last observation day spent most of the time away from the cliff and were observed infrequently. The quarry was again visited on 18, 22, and 27 July, for 30 min each day, to check if any fledglings were present or any radiotransmitter signal could be detected. No fledglings were seen and no radiotransmitter signal was detected after 18 July.

Behavioral observations were dictated on a tape. Every 30 min the perching location of every fledgling on the cliff was recorded. Distances between each fledgling and its nest, nearest sibling, and nearest unrelated fledgling were estimated later on an enlarged photo of the cliff with 0.5 m precision. I considered that fledglings were perched in groups when distance between fledglings was <2 m.

The age of 15 of the chicks at the time of banding was estimated from the equation: Age (d) = $8.14 + 0.17 \times 8\text{th primary length (mm)}$, obtained from growth data of common kestrel chicks in central Spain (Veiga 1985). Fledging age was the first day a chick was seen flying or on a perch it had to reach flying. I considered the date of independence of a fledgling to be the mean between the last day the fledgling was seen at the colony and the first day the fledgling was no longer seen. Radio-tagged fledglings showed that not all fledglings present at the colony were observed on every 4-hr period, indicating that the duration of the post-fledging dependence period of fledglings without radiotransmitters could have been underestimated. Fledglings with radiotransmitters, even if they were not seen, were considered still dependent if their signals could be located at the colony. None of the fledglings with radiotransmitters were observed or located by telemetry after leaving the colony cliff for the first time.

I believe no radiotransmitters were lost, but some fledglings could have died before independence. I found remains of at least one unidentified fledgling eaten by a predator.

RESULTS

Common kestrel chicks fledged at a mean age of 31 d (range 27–36 d, SD = 2.8, $N = 15$). There were no significant differences in fledging age be-

tween fledglings with radiotransmitters ($\bar{x} = 33$ d, $N = 4$) and those without ($\bar{x} = 30.5$ d; $t = 1.46$, $df = 13$, $P = 0.17$). Fledglings became independent on average 16 d after fledging (range 8–25 d, SD = 5.2, $N = 20$), and there were no differences between fledglings with radiotransmitters ($\bar{x} = 15.5$ d, $N = 5$) and those without ($\bar{x} = 16.1$ d; $t = -0.21$, $P = 0.83$). Neither fledging date ($F = 1.02$, $df = 1, 18$, $P = 0.31$), fledging age ($F = 0.085$, $df = 1, 13$, $P = 0.78$), brood-size ($F = 0.446$, $df = 2, 17$, $P = 0.65$) nor order within the brood ($F = 1.683$, $df = 4, 9$, $P = 0.24$) had any significant effect on the duration of the post-fledging dependence period. Fledglings of the same brood did not become independent on the same day and the maximum difference in independence dates within a brood averaged 11.6 d (SD = 5.6, $N = 5$). Two banded chicks without radiotransmitters were never observed at the colony after fledging and probably died before independence (9% mortality, $N = 22$).

Fledgling Behavior. Common kestrel fledglings returned infrequently to their nests after fledging (only 4% of the observations were at <2 m from the nest). They perched on the ledges and on top of the cliff, alone (54% of observations) or in groups (46% of observations, $N = 307$). Groups ranged from 2–5 fledglings ($\bar{x} = 3.6$ fledglings, SD = 1.4, $N = 76$) and most of them, 84%, included fledglings from different broods. Of 20 marked fledglings observed, 19 were seen at least once in a group with unrelated fledglings. Fledglings perched closer to unrelated fledglings than to their nest (paired t -test for median distances, $t = 2.11$, $df = 14$, $P = 0.049$), or to their siblings ($t = 2$, $df = 14$, $P = 0.06$), although the last difference was not significant. Median distance to the nearest sibling was not significantly different from median distance to the nest ($t = -0.99$, $df = 18$, $P = 0.34$; Fig. 1).

Fledglings frequently begged for food, perched or in flight, from any adult kestrel coming to the colony. On at least six instances they begged for food unsuccessfully from lesser kestrels. I also observed four juveniles eating insects 4–13 d after fledging. Although the capture was not witnessed, adults were never observed delivering insects to the fledglings.

I observed four fledglings engaged in play behavior with objects 16, 16, and 18 d after fledging. The age of the fourth bird was unknown. On separate occasions two fledglings flew low over the cliff performing prey catching and plucking movements on small roots hanging from the cliff. A similar behavior

was performed on a small twig, a stone, and an airborne feather in quick succession by another fledgling. The fourth fledgling performed prey plucking movements on an object carried with its talons. The most frequent play behavior were fast flight chases by two or more fledglings. Fledglings chased each other and dove toward other fledglings perched on the cliffs making them fly. The roles between chaser and chased changed frequently, suggesting some kind of social play. Chases among fledglings—from the same and different broods—were observed on 15 occasions, 5–13 d after fledging.

Beaking, a behavior in which one individual nibbles at the beak and lore area of another (Sherrod 1983), was observed in one instance between two fledglings from different broods. Fledglings were observed hovering for the first time a mean of 9.7 d after fledging (SD = 6.5, $N = 10$).

Adult Behavior. Adult common kestrels were only seen at the colony when delivering prey to the fledglings. Both male and female adults fed the fledglings during the post-fledging dependence period. Of 22 prey deliveries in which the sex of the adult was recorded, nine were performed by males and 13 by females. Twice a male was seen transferring the prey to the female before she fed the fledglings. No aerial prey transfers to fledglings were observed, and all prey transfers took place on cliff perches or on the ground. After all chicks had fledged, 85.3% of the prey transfers took place on perches different from the nest ($N = 34$). All prey delivered were birds and small mammals. The average prey delivery rate by adult common kestrels at the colony was 0.9 prey/hr. Correcting for the number of fledglings present, each fledgling received an average of 1.1 prey/d. After young fledged, adults frequently transferred prey to groups of fledglings from more than one nest. Adults did not seem to select the fledgling in the group to which they transferred the prey. As adults were not marked, it was not clear if adults were feeding only their offspring or occasionally feeding other fledglings.

Aggression. I never observed aggressive behavior among common kestrel fledglings. Most of the aggressive behavior observed was allospecific. A lesser kestrel adult female took 0.5 hr to expel a common kestrel fledgling from her nest that had accidentally landed there. An adult common kestrel attacked a lesser kestrel female who had previously attacked a common kestrel fledgling. An adult male common kestrel dove four times toward a fledgling who was

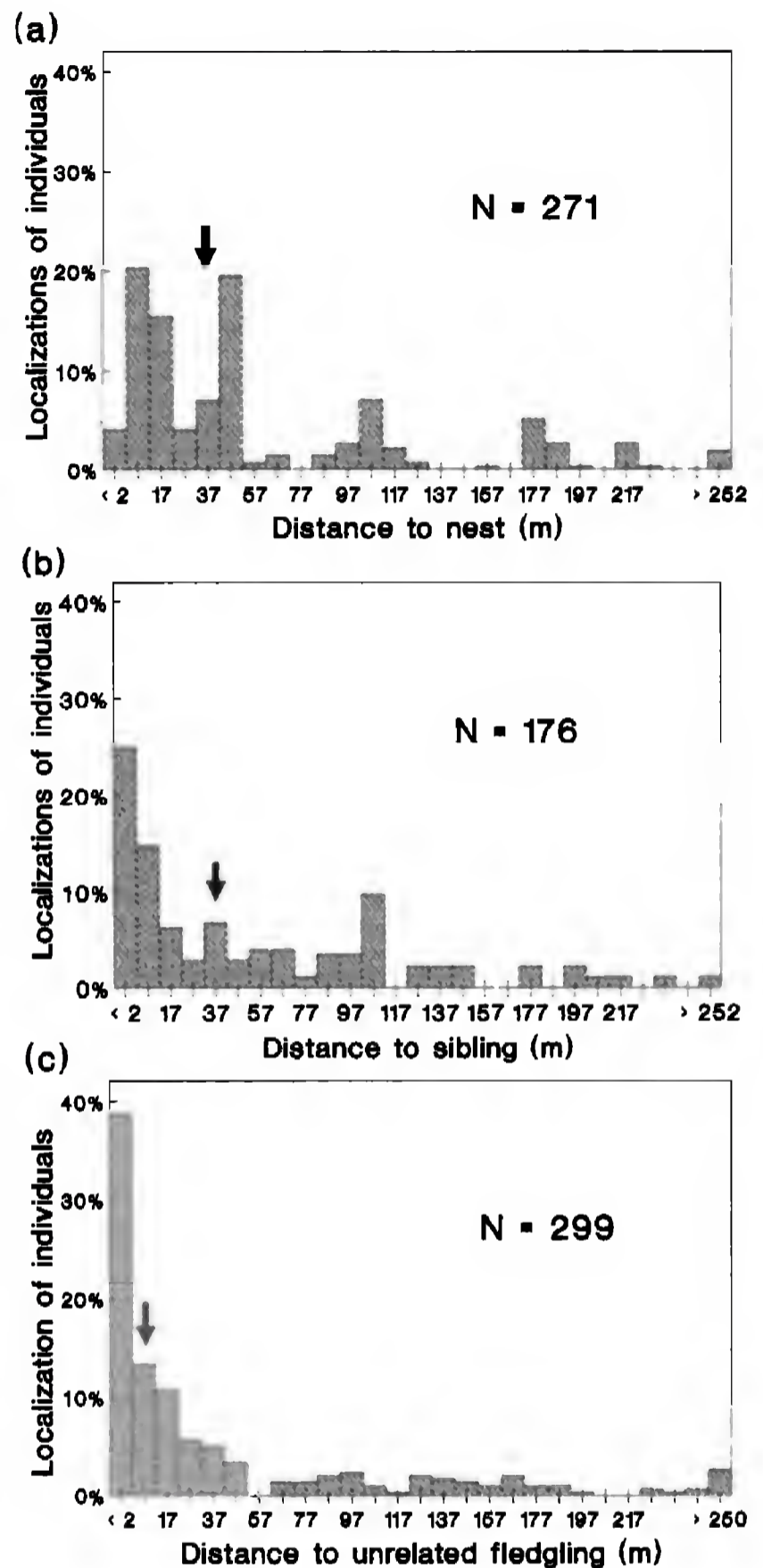


Figure 1. Frequency distribution of the observations of perched common kestrel fledglings in relation to distance to their nest (a), distance to the nearest sibling (b), and distance to the nearest unrelated fledgling (c), during the post-fledging dependence period. Data on all fledglings were pooled. The values are given in 5 m intervals, except the first interval, <2 m, and the last interval, >252 m. Arrows indicate the medians. Distances were measured every 30 min with 0.5 m precision.

begging in a fluttering flight after him and forced the fledgling to perch on the cliff.

DISCUSSION

Common kestrel chicks fledged in southwestern Spain at an average age of 31 d, similar to that reported by other authors in Europe (27–32 d; Cramp and Simmons 1980) and in Africa (34 d; Steyn 1982). The average duration of the post-fledging dependence period I observed, 16 d, was shorter than those reported both in Europe (20–25 d, Tinbergen 1940; 1 mo, Cramp and Simmons 1980; 30 d, Masman 1980 in Komen and Myer 1989), and in Africa (1 mo, Steyn 1982; 41.5 d, Komen and Myer 1989).

I do not think that the kestrel family groups I observed continued together somewhere else after leaving the colony. Siblings would have disappeared on the same day, but they did not. It is still possible that I underestimated the post-fledging dependence period of the fledglings without radiotransmitters, because on average only 66% of the dependent fledglings were observed on each 4-hr period. Also, the death of some fledglings before independence could have remained unnoticed, but the mean duration of the post-fledging period of the five fledglings with radiotransmitters was not significantly different from that of the fledglings without. This supports the idea that I did not underestimate the duration of the post-fledging dependence period.

Some species of raptors have shorter post-fledging dependence periods in populations breeding at higher latitudes (Bustamante 1993, unpubl. data). The high variability among individuals in the duration of the post-fledging dependence period, small sample sizes in all studies, and this latitudinal effect probably explain the high variability among estimates from different authors. Also, the short post-fledging dependence period I observed could be related to the conditions (possibly, high abundance of prey) that permit that common kestrels nest colonially in this area.

My observations also confirm that the nest is rarely used by common kestrels after fledging (Tinbergen 1940), and that fledglings play with objects during the post-fledging period (Komen and Myer 1989), possibly as a way to develop and train their hunting skills. Also, the first prey caught were insects as observed by Komen and Myer (1989), and this has been observed in many other species of raptors (e.g., Baker-Gabb 1978, Mueller et al. 1981, Sherrod 1983, Oliphant and Tessaro 1985, Varland et al. 1991,

Lawrence and Gay 1991, Varland and Loughin 1992).

Although Newton (1979) contended that most fledgling raptors perch apart from their siblings, common kestrel fledglings perched close to each other, were never aggressive toward other fledglings, and engaged in social behavior (beaking) and social play (chases) with their siblings and with other fledglings. Siblings of other species of falcons also socialize during the post-fledging dependence period. Allopreening and beaking have also been observed (Sherrod 1983, Lett and Bird 1987, Varland et al. 1991, Varland and Loughin 1992).

Fledglings from different broods intermingled during the post-fledging dependence period because nests were close and fledglings did not avoid perching close to fledglings from other broods. Groups of fledglings were not caused by fledglings trying to stay close to their own nests, where it could be expected that parents came with prey, or by fledglings trying to maintain a close group with their siblings at some point on the cliff, where they could be easily found and fed by their parents.

Adults provided prey to fledglings that were usually in groups and did not seem to be able to select who finally obtained the prey. They never behaved aggressively toward fledglings and never chased fledglings from other broods away from the vicinity of their nests, in contrast to what has been observed in the colonial lesser kestrel (Bustamante and Negro in press). Also fledglings were not selective to whom they directed their begging. All this suggests that adults could have accidentally provided food to fledglings that were not their own. Even lesser kestrels, which seem to be able to recognize their offspring after fledging and behave aggressively toward unrelated juveniles near their nests, have been recorded accidentally feeding fledglings from other nests (Bustamante and Negro in press) and adopting unrelated nestlings (Donázar et al. 1991, J.L. Tella pers. comm.).

The capacity to recognize its own offspring after fledging could be less developed in the common kestrel than in the lesser kestrel. The common kestrel is generally territorial and a solitary nester. Breeding colonies, like the one I studied, are uncommon (Cramp and Simmons 1980, Village 1990). It is probably not necessary for common kestrels to discriminate between their offspring and unrelated juveniles during the post-fledging dependence period under normal circumstances, and hence the lack of

adult discrimination of offspring and lack of aggression toward unrelated fledglings I observed in this colony.

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GOSHAWK DIET IN A MEDITERRANEAN AREA OF NORTHEASTERN SPAIN

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ABSTRACT.—The diet of the goshawk (*Accipiter gentilis*) is described throughout the year in La Segarra, a Mediterranean area of Catalonia (NE Spain) where one of the densest goshawk populations recorded in Europe was found. Red-legged partridge (*Alectoris rufa*), European rabbit (*Oryctolagus cuniculus*), wood pigeon (*Columba palumbus*), jay (*Garrulus glandarius*), magpie (*Pica pica*), thrushes (*Turdus* spp.) and red squirrel (*Sciurus vulgaris*) formed the bulk of the goshawk diet. Nestling and fledgling birds were very important during the breeding period, but the rabbit was the main source of biomass for most of the year, especially in winter. In the breeding season, pairs in heavily forested areas captured more squirrels and less rabbits than those in lightly forested areas. Changes in the diet involving a decrease in rabbit consumption and an increase in the proportion of red-legged partridge were detected following a rabbit population crash caused by the viral haemorrhagic disease.

KEY WORDS: *Accipiter gentilis*; goshawk; Spain; Mediterranean; food habits.

Dieta del azor en una zona mediterránea del noreste de España

RESUMEN.—Se describe la dieta del azor (*Accipiter gentilis*) a lo largo del año en la Segarra, una zona mediterránea de Cataluña (NE de España) donde se encontró una de las poblaciones más densas de azor hasta ahora registradas en Europa. La perdiz roja (*Alectoris rufa*), el conejo (*Oryctolagus cuniculus*), la paloma torcaz (*Columba palumbus*), el arrendajo (*Garrulus glandarius*), la urraca (*Pica pica*), los zorzales y mirlos (*Turdus* spp.) y la ardilla (*Sciurus vulgaris*) fueron las presas principales. Las aves jóvenes constituyeron una buena parte de las presas del azor durante el período reproductor, pero el conejo fue la principal fuente de biomasa durante la mayor parte del año, especialmente en invierno. Las parejas de las zonas más forestadas capturaron más ardillas y menos conejos que las parejas de las zonas abiertas. La drástica reducción de las poblaciones de conejo como consecuencia de la neumonía hemorrágica vírica, condujo a una disminución de su consumo y a un aumento del de perdiz.

The food habits of the goshawk (*Accipiter gentilis*) have been described in northern and central Europe (e.g., Sulkava 1964, Opdam et al. 1977, Wikman and Tarsa 1980, Marquis and Newton 1982, Goszczyński and Pilatowski 1986, Widén 1987), but not in the Mediterranean region. Although there are some general descriptions of goshawk food habits from several regions of Spain (Morillo and Lalanda 1972, Veiga 1982, Garrigues et al. 1990, Mañosa et al. 1990), these are limited to the breeding season and a detailed study on this subject in a Mediterranean area is still lacking. The objectives of this paper are (1) to describe the diet of a goshawk population in a Mediterranean area of Catalonia, (2) to analyze diet changes throughout the year, and (3) to study diet variation in relation to changes in prey availability between habitat types and years.

STUDY AREA AND GOSHAWK POPULATION

The study area was within the universal transverse mercator squares 31TCG50, 31TCG51, 31TCG60,

31TCG61, and 31TCF59 in La Segarra County in the northeastern portion of the Iberian peninsula. The relief of the area is tabular, altitude lies between 500–800 m, and the climate is a transition between continental Mediterranean and submediterranean. Natural vegetation communities cover only 30% of the area, the remainder being occupied mainly by cereal crops. Depending on the exposure and soil characteristics, different types of secondary pine forest (*Pinus nigra*, *P. sylvestris*, and *P. halepensis*) or oak forest (*Quercus faginea* and *Q. ilex*) cover the areas not suitable for agriculture. The southern and eastern parts of the study area are more forested, while the northern and western parts are mostly devoted to crops. Nest sites were classified as heavily forested if more than 50% of the area within a 1-km radius of the nest was covered by wood or lightly forested if that percentage was less than 50%.

From 1987–89 the maximum number of goshawk pairs nesting simultaneously in a well-searched 176 km² area was 22, but the estimated total population from the patterns of use and distribution of nest sites was 26 pairs, giving a maximum density of 1 pair/6.8 km², one of the highest in Europe (see Kalchreuter 1981, Thissen et al 1981, Bijlsma 1991). The mean nearest-neighbor distance between the geometric mean locations of the nesting sites

Table 1. Percentage of prey obtained when analyzing goshawk diet by different methods (see Methods section) during the nestling period at two nests in 1989. (N = number of prey individuals.)

	OBSER- VATIONS FROM HIDE $N = 74$	NEST REMAINS $N = 82$	PELLETS $N = 29$	MIXED $N = 102$
Reptilia	0.0	1.2	0.0	1.0
Phasianidae	21.6	25.6	6.9	21.6
Columbidae	18.9	15.8	17.2	17.6
Estrigiformes	0.0	2.4	0.0	2.0
Picidae	1.3	1.2	17.2	4.9
Turdidae	17.6	11.0	0.0	8.8
Corvidae	17.6	15.8	20.7	14.7
Sturnidae	0.0	3.7	6.9	4.9
Other Passer.	9.5	3.7	6.9	4.9
Other birds	4.0	2.4	3.4	2.9
Leporidae	4.0	14.6	10.3	11.8
Sciuridae	5.4	2.4	10.3	4.9

of every pair was 1535 m (SD = 455 m, range = 825–2800 m, $N = 26$). Pair dispersion, measured by the G statistic (Brown and Rothery 1978), showed a value of 0.844, indicating a regular distribution of pairs (Tjernerberg 1985). The average laying date during the 1986–90 period, estimated by inspection of the nests every two days from mid-March until the first egg was laid, was 5 April \pm 7.96 d ($N = 73$, range = 21 March–29 April).

METHODS

Prey Identification and Classification. Prey remains, bones, fur, nails and feathers found on nests, plucking sites and pellets were identified by macroscopic comparison with skeleton and skin reference collections. Arthropods were only considered as possible goshawk prey when found on the nests, but not in pellets, and were identified to taxonomic order. I tried to identify all vertebrate remains to species. When possible, the sex and age of prey was recorded. For nidicolous birds, I considered three age categories: nestlings, fledglings, and adults. Young red-legged partridges (*Alectoris rufa*) were considered nestlings if their size was less than three-fourths the adult size and fledglings if larger. Assigning avian prey to age class was based on size, plumage, feather characteristics, and degree of ossification. The adult category might have included some young birds no longer distinguishable from adults. European rabbits (*Oryctolagus cuniculus*) and red squirrels (*Sciurus vulgaris*) were classified as young or adult according to size or degree of ossification. When a prey could not be classified to age, it was not considered in the age selection analysis. Prey found complete or nearly complete were weighed with a spring balance. Otherwise, the live biomass was estimated using bibliographic information (Geroudet 1946–57) or data from the study area according to the age and, if necessary, sex of the prey. No wastage

was considered, therefore the biomass figures in this paper refer to captured biomass.

Quantification of Diet During the Breeding Season. Between 1985–89, I studied nestling diet (May–July) by repeated visits to nest sites to collect all prey remains (feathers, fur, and bones) and pellets at the nests and known plucking sites. Recently delivered or partially eaten prey were recorded as prey remains, but not collected. In 1985 and 1986 nest visits were sporadic. From 1987–89, all nests containing chicks were visited every 4 d from hatching to a few days after fledging. To minimize disturbance, sampling was reduced during the laying and incubation periods (April).

The identity of the prey remains and the minimum number of prey individuals necessary to explain their presence was established for each visit, according to the number of bones or flight feathers encountered. All pellets from a visit were pooled into a single sample and analyzed together. The presence of different prey types in these samples was recorded, but no attempt was made to quantify the number of individuals represented. To avoid counting the same prey individual twice in the same visit (i.e., in remains and in pellets), prey found in pellets were computed only if they had not been found as remains in the same visit. I avoided counting the same prey individual in successive visits by comparing prey from successive collections: prey found in pellets or as an old remain were not considered if they had been detected in the previous visit as a fresh or partially eaten prey. In both cases, however, all methods of detection were recorded.

To assess the reliability of the method noted above, 322.5 hours were spent observing in hides installed 15–20 m away from two nests in 1989. During the nestling period, observation started at 1200 H, lasted until 1900 H and was continued the following day from 0500–1200 H. The process was alternated between the two nests until the young fledged. Only prey observed being delivered to the nest were recorded and identified with the aid of a 20–60 \times telescope. Sixty-seven out of 74 (90.5%) prey were identified to the species. The remaining seven prey were either unidentified small passerines or nestling birds. The results of these observations, which were assumed to be an unbiased sample of the nestling diet, were compared with the results obtained at the same nests and year by pellet counts alone, prey remains alone, and the combination of both as described above. The results given by none of these methods were significantly different from those obtained by direct observation, but the combined method gave the nearest approximation ($\chi^2 = 7.50$, df = 6, $P = 0.277$; $\chi^2 = 11.47$, df = 6, $P = 0.075$; $\chi^2 = 6.09$, df = 6, $P = 0.412$, respectively; Table 1). However, it still overestimated the percentage of rabbits in the diet and underestimated the proportion of thrushes (*Turdus* sp.) and other small birds (Table 1).

Quantification of Diet Outside the Breeding Season. Diet outside the breeding season (August–March) was studied from 1986–88 by looking for prey remains at plucking sites (Opdam et al. 1977, Ziesemer 1983). I tried to standardize the scanning pattern over different months and to avoid finding prey of common buzzards (*Buteo buteo*) or sparrowhawks (*Accipiter nisus*) by scanning only goshawk nesting areas. Two monthly inspections were

Table 2. Prey items of goshawk in La Segarra during 1987–89. Weight in grams. Species with *N* < 10 are grouped and listed underneath.

	<i>N</i> (%)	TOTAL WEIGHT (%)
Arthropods ^a	8 (0.40)	17 (0.00)
Reptiles	21 (1.05)	2906 (0.51)
<i>Lacerta lepida</i>	18 (0.90)	2728 (0.48)
Other reptiles ^b	3 (0.15)	178 (0.03)
Birds	1519 (75.85)	326 502 (56.90)
<i>Alectoris rufa</i>	362 (18.07)	140 845 (24.54)
<i>Coturnix coturnix</i>	21 (1.05)	2100 (0.37)
<i>Columba palumbus</i>	196 (9.79)	67 169 (11.70)
<i>Columba livia</i>	13 (0.65)	3950 (0.69)
Unidentified pigeon	39 (1.95)	11 470 (2.00)
<i>Streptopelia turtur</i>	28 (1.40)	3920 (0.68)
<i>Otus scops</i>	27 (1.35)	2160 (0.38)
<i>Athene noctua</i>	18 (0.90)	3060 (0.53)
<i>Picus viridis</i>	31 (1.55)	6160 (1.07)
<i>Picoides major</i>	15 (0.75)	1200 (0.21)
<i>Turdus merula</i>	134 (6.69)	10 989 (1.91)
<i>Turdus viscivorus</i>	38 (1.90)	4232 (0.74)
Unidentified thrush	25 (1.25)	1887 (0.33)
<i>Garrulus glandarius</i>	184 (9.19)	28 197 (4.91)
<i>Pica pica</i>	54 (2.70)	9345 (1.63)
<i>Sturnus vulgaris</i>	79 (3.94)	6516 (1.14)
<i>Fringilla coelebs</i>	23 (1.15)	529 (0.09)
Unidentified passerine	87 (4.34)	3504 (0.61)
Unidentified bird	36 (1.80)	3190 (0.56)
Other birds ^c	109 (5.44)	16 079 (2.80)
Mammals	455 (22.72)	244 486 (42.60)
<i>Oryctolagus cuniculus</i>	333 (16.63)	220 526 (38.43)
<i>Sciurus vulgaris</i>	86 (4.29)	21 330 (3.72)
Other mammals ^d	36 (1.79)	2630 (0.46)
Total	2003	573 858

^a Arthropods: *Scolopendra* sp., Orthopterans, Coleopterans.
^b Other reptiles: *Anguis fragilis*, *Psammodromus algirus*, unidentified reptiles.
^c Other birds: *Accipiter gentilis* (nestlings from the same nest), *Accipiter nisus*, *Phasianus colchicus*, *Scolopax rusticola*, *Gallinula chloropus*, *Columba oenas*, *Clamator glandarius*, *Cuculus canorus*, *Tyto alba*, *Strix aluco*, unidentified owls, *Caprimulgus europaeus*, *Caprimulgus* sp., *Merops apiaster*, *Upupa epops*, *Galerida* sp., *Lullula arborea*, unidentified lark, *Luscinia megarhynchos*, *Turdus philomelos*, *Sylvia* sp., *Parus caeruleus*, *Parus major*, *Certhia brachydactyla*, *Oriolus oriolus*, *Lanius excubitor*, *Corvus corone*, unidentified crow, *Passer domesticus*, *Serinus serinus*, *Carduelis carduelis*, unidentified Fringillidae, *Miliaria calandra*.
^d Other mammals: *Crocidura russula*, *Eliomys quercinus*, *Microtus duodecimcostatus*; *Apodemus sylvaticus*, *Mus spretus*, *Rattus norvegicus*, *Rattus rattus*, unidentified mice, unidentified rodents.

made at 10 previously selected sites, but fresh remains found in sporadic visits to other nesting areas were also recorded. I recorded all fresh kills, bones, fur or feathers found, and established the minimum number of prey necessary to explain their presence according to the number of bones and flight feathers found. Because of the characteristics of the autumn and winter common buzzard diet in Catalonia, consisting mainly of small mammals and invertebrates (Mañosa and Cordero 1992), little confusion should have arisen with that species. However, some spar-

rowhawk prey could have been confused with goshawk prey. They can be distinguished by the extent of the feather plucking (larger and usually scattered in the goshawk) and the presence of legs or bill remains left by the sparrowhawk (Opdam 1975). When the predator identity could not be established with confidence, the prey was not considered.
Prey Availability Counts. European rabbit counts were carried out at dusk 1–5 times each month. A 19.7-km route (A) across the whole study area was covered with a

vehicle, at a maximum speed of 40 km/h, from July 1987 to December 1989. All rabbits seen on the route were recorded and abundance was expressed as number of rabbits seen per kilometer. Another 25.4-km route (B), covering only the south of the study area, had been traversed in the same way between October 1986–October 1988. The results of the counts during the period when both transects were conducted simultaneously (July 1987–October 1988) were used to obtain a conversion index between them, which was used to obtain an estimate of rabbit abundance for the whole area from October 1986–June 1987 from counts conducted in route B. To obtain rough estimates of red-legged partridge abundance, I conducted car counts in April and May during the morning or before dusk, at a maximum speed of 20 km/h. A total of 57 km in 10 counts of different length and location within the study area were done in 1987 and 102 km in 19 different counts in 1989. Results were expressed as number of partridges seen per kilometer.

Data Analysis and Statistics. Chi-square tests were used to compare diet composition by numbers of prey at different times of the year, and one-way analysis of variance (ANOVA) combined with the Scheffe's test (Zar 1984) were used to compare average prey weights. Variations in the diet of the 1987–89 breeding seasons were analyzed by habitats (heavily forested versus lightly forested) and years. Prey were sorted according to the different nest sites and years. Samples containing less than 20 prey were discarded (to reduce bias caused by differential sampling), leaving 34 diet samples from 18 different nest sites, totaling 1590 prey items. The coefficient of variation between samples in the percentage of each prey type in each sample was calculated to determine the degree of homogeneity in the consumption of different groups of prey. Chi-square tests for mutual and partial independence in three-dimensional tables were performed following Zar (1984). When a two-dimensional chi-square test was globally significant, observed cell frequencies were considered to be significantly different from the expected frequencies when the absolute value of the standardized residual was $>Z_{\alpha/2}$. Statistical significance level was set at $\alpha = 0.05$. Statistical analyses were performed with SPSS (1990). The Shannon-Weaver index (H' , log base 2) was used to describe dietary diversity (Margalef 1982). When appropriate, mean \pm standard deviation are indicated.

RESULTS

General Diet Description. Samples for the nestling period (May–July) included 27 prey items in 1985–86, 391 prey items from 13 nests in 1987, 871 prey items from 26 nests in 1988 and 452 prey items from 12 nests in 1989. Only 23 prey items were obtained during the laying and incubation periods (April), and 239 prey were determined for the August–March period.

The diet of goshawks in La Segarra included 61 different types of prey (Table 2). Prey weight ranged from only a few grams to more than 1000 g for some adult rabbits. The average weight of prey was 286

± 235 g ($N = 2003$). Arthropods were incidental and in no case did we have evidence that they had been captured by the goshawk (i.e., they could be prey of goshawk prey). Reptiles were only consumed during the nestling period. The diet consisted almost exclusively of endothermic vertebrate prey (98.9%). Red-legged partridge, European rabbit, wood pigeon (*Columba palumbus*), jay (*Garrulus glandarius*), magpie (*Pica pica*), blackbird (*Turdus merula*), European starling (*Sturnus vulgaris*) and red squirrel formed the 71.3% of goshawks' captures. In terms of biomass, the rabbit was the basic prey, followed by the red-legged partridge and the wood pigeon, which altogether accounted for 74.7% of the captured biomass.

Seasonal Variation. Only 1898 prey individuals could be assigned to a particular month of the year. Frequencies of capture varied significantly by season ($\chi^2 = 144.34$, $df = 28$, $P < 0.001$; Table 3). Rabbits and passerines accounted for more than 64% of the prey in the January–April period. In May and June passerines and game birds were the main prey, but rabbits, pigeons, and corvids were also important. In July, passerines lost their preponderant position in the diet and game birds made up the largest proportion of it, followed by pigeons, corvids and rabbits. In the August–December period rabbits were again the main prey, followed by pigeons and game birds. In terms of biomass, much less variation occurred, the rabbit being the dominant prey throughout the year, especially outside the breeding season. Game birds had a peak contribution in May, pigeons in the July–December period, and corvids in the June–July period.

Globally, diet was more diverse and contained smaller prey during the nestling period (May–July, Table 3). ANOVA showed significant differences in the average weight of prey between periods ($F_{4,1893} = 16.63$, $P < 0.01$), being lower in May, June and July than in the January–April and August–December periods (Table 3). Between May and July, nestling and fledgling birds accounted for 37.5% of the 781 birds for which age could be determined, or 18.1% of biomass (185 kg). Extrapolating to all prey, 28.8% of prey and 10.8% of the total biomass captured were young birds. The proportion of immature birds (both nidicolous and precocial) in relation to fully grown ones increased from the beginning of May to the end of July ($\chi^2 = 32.38$, $df = 5$, $P < 0.001$; Fig. 1) as the nesting season progressed. For nidicolous birds alone, the proportion of nestlings

Table 3. Percentages by numbers (*N*) and weight (*W*) of different prey categories found in the diet of the goshawk at different times of the year in La Segarra. (Only *N*% were tested for significance.)

	JAN-APRIL		MAY		JUNE		JULY		AUG-DECEMBER	
	<i>N</i>	<i>W</i>	<i>N</i>	<i>W</i>	<i>N</i>	<i>W</i>	<i>N</i>	<i>W</i>	<i>N</i>	<i>W</i>
Phasianidae	13.4	16.3	22.4	35.3	17.0	24.6	21.5	17.4	20.3	19.6
Columbidae	14.9	14.4	10.5	12.9	12.8	13.6	16.5	18.8	21.9 ^a	21.1
Corvidae	0.7 ^a	0.4	9.4	5.3	14.6 ^a	8.4	16.2 ^a	10.5	8.6	3.5
Passeriformes	29.1	4.0	28.3 ^a	7.3	22.7	5.8	12.8 ^a	3.5	12.5 ^a	2.1
Other birds	2.2 ^a	1.1	4.7 ^a	1.6	9.9	6.5	12.1 ^a	5.8	7.8	3.2
Leporidae	35.1 ^a	60.9	15.0	30.8	14.3	35.3	14.5	40.3	26.6 ^a	49.9
Sciuridae	2.2	1.4	5.6	5.0	5.0	4.7	3.4	3.2	0.8 ^a	0.5
Other prey	2.2	1.3	4.0	1.7	3.7	1.0	3.0	0.2	1.6	0.1
Number of prey	134		446		893		297		128	
Total weight (kg)	53.1		122.4		240.7		76.9		50.5	
Average weight (g)	396 ± 276		274 ± 207		270 ± 235		259 ± 241		395 ± 256	
<i>H'</i>	2.26		2.70		2.83		2.80		2.57	

^a Significantly different from expected frequency.

decreased and that of fledglings increased throughout the breeding season (May 32.8% and 14.3%, *N* = 119; June 21.3% and 27.1%, *N* = 314; July 13.6% and 28.8%, *N* = 66, respectively; $\chi^2 = 14.65$, *df* = 4, *P* < 0.005). The proportion of nestling corvids decreased from May to July as the proportion of fledglings increased ($\chi^2 = 23.66$, *df* = 4, *P* < 0.01; Fig. 2). The proportion of young partridges captured increased from May (0%) to July (74.6%, $\chi^2 =$

124.80, *df* = 2, *P* = 0.01; Fig. 2). Similar but non-significant trends were found for pigeons and starlings, while thrushes showed a reverse trend (Fig. 2). The proportion of young to adult rabbits in May (100%, *N* = 38), June (69.6%, *N* = 79) and July (59.1%, *N* = 22) showed a significant decrease ($\chi^2 = 17.33$, *df* = 2, *P* < 0.01). The proportion of young to adult squirrels in May (20%, *N* = 5), June (13%, *N* = 8) and July (0%, *N* = 5) did not show a significant trend ($\chi^2 = 1.04$, *df* = 2, *P* = 0.594).

Year-to-year and Habitat Variation. Significant variation in diet composition occurred between the 34 samples analyzed ($\chi^2 = 392.62$, *df* = 231, *P* < 0.001). According to the coefficients of variation of the different prey groups, game birds (C.V. = 31.2%), passerines (C.V. = 36.2%) and corvids (C.V. = 43.3%) were the prey more homogeneously represented in the samples, whereas squirrels (C.V. = 89.2%) and other prey (C.V. = 105.8%) were the most unevenly consumed groups. Pigeons (C.V. = 51.1%), rabbits (C.V. = 57.9%) and other birds (C.V. = 74.6%) showed intermediate levels of variation. Year-to-year and habitat differences in prey availability might be partially responsible for this variation. A test for mutual independence of prey composition, year, and habitat showed dependence of all three variables ($\chi^2 = 132.69$, *df* = 37, *P* < 0.001). Test for partial independence showed habitat being dependent on year and prey ($\chi^2 = 94.90$, *df* = 23, *P* < 0.001), year being dependent on prey and habitat ($\chi^2 = 70.82$, *df* = 30, *P* < 0.001) and prey being dependent on habitat and year ($\chi^2 = 121.93$, *df* =

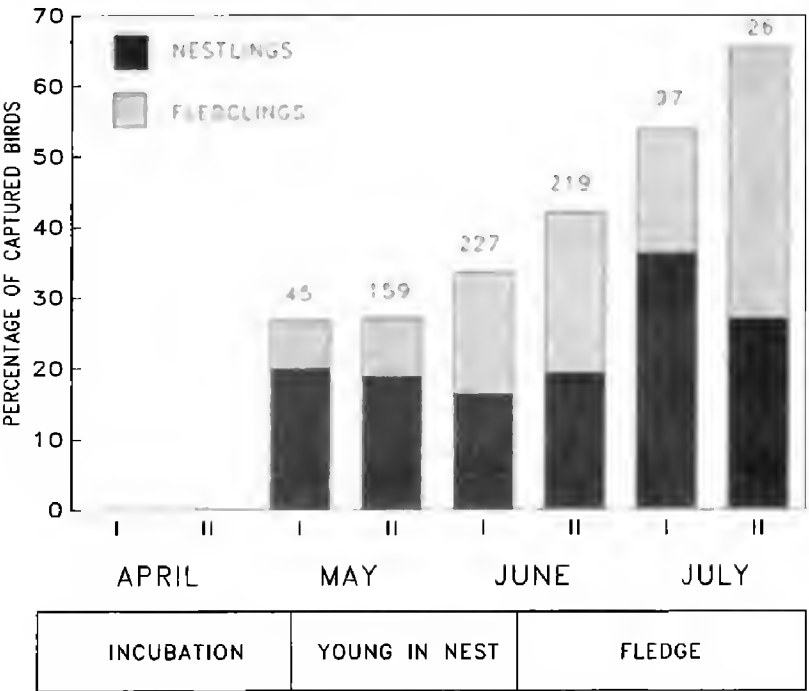


Figure 1. Proportion of young birds in relation to all birds (nidicolous and precocial) captured by goshawks in successive 2-wk periods during the breeding season. Numbers above the bars refer to the sample size used to estimate age composition in each case. The approximate timing of goshawk breeding is shown underneath.

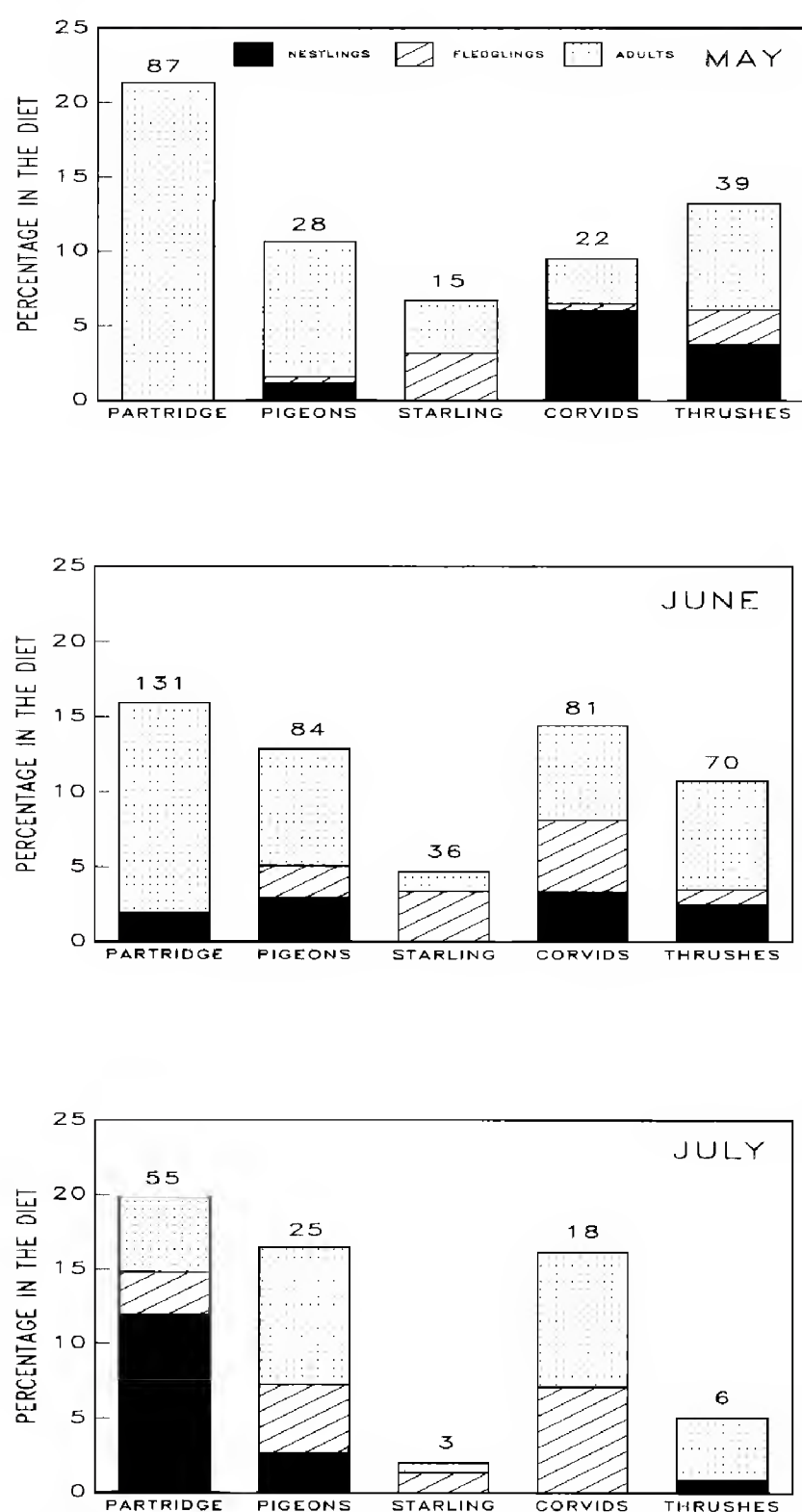


Figure 2. Percentages of nestlings, fledglings, and adult birds of some relevant groups in the diet of the goshawk in May, June, and July. Numbers above the bars refer to the sample size used to estimate age composition in each case.

35, $P < 0.001$). In consequence, three two-dimensional tables comparing diet between habitats independently for each year, and two two-dimensional tables comparing diet between years independently for each habitat were tested. In all three years, diet differences between heavily forested and lightly forested areas were statistically significant (1987, $\chi^2 = 21.53$, $df = 7$, $P = 0.003$; 1988, $\chi^2 = 39.39$, $df = 7$, $P < 0.001$; 1989, $\chi^2 = 18.83$, $df = 7$, $P = 0.009$;

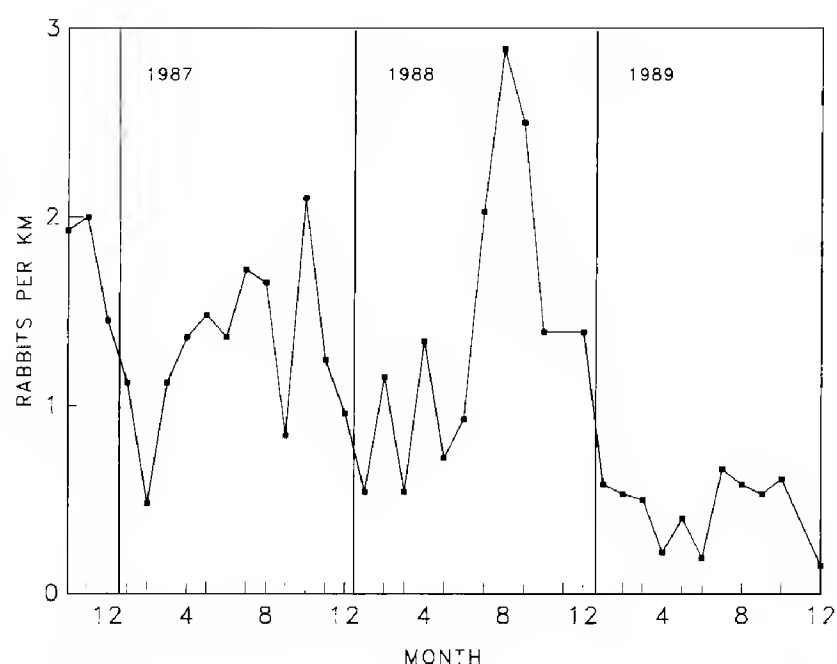


Figure 3. Changes in the index of European rabbit (*Oryctolagus cuniculus*) availability in La Segarra during the period 1986-89.

Table 4). When the three years were pooled, differences between habitats remained significant ($\chi^2 = 66.24$, $df = 7$, $P < 0.001$). Compared with lightly forested areas, diet in heavily forested areas included significantly less rabbits and more squirrels (Table 4). Habitat differences in the proportion of game birds, pigeons, corvids and passerines were non-significant, but consistent between years. Although the trends were similar in both habitats, year-to-year variation was significant in the lightly forested area ($\chi^2 = 33.69$, $df = 14$, $P = 0.002$) but not in the heavily forested area ($\chi^2 = 21.54$, $df = 14$, $P = 0.09$). A decrease in dietary diversity was noticed in both areas in 1989. After pooling the two habitats, differences between years remained significant ($\chi^2 = 41.84$, $df = 14$, $P < 0.001$). Diet in 1987 was characterized by a higher proportion of corvids, while diet in 1989 was characterized by a decrease in the proportion of rabbits and an increase in that of game birds (Table 4). The changes detected in 1989 followed a decline in the availability of rabbits (Fig. 3), whereas partridge availability had remained constant throughout the study period (1987: 1.02 partridges/km; 1989: 0.94 partridges/km).

DISCUSSION

The diet of the goshawk in La Segarra showed three main peculiarities when compared to other European areas: (1) presence of reptiles, (2) high proportion of red-legged partridges, and (3) high proportion of rabbits. The first characteristic was also found in all Iberian localities studied (Morillo

Table 4. Goshawk diet variation in La Segarra according to year and habitat. (L: lightly forested area; H: heavily forested area.)

	1987		1988		1989	
	L	H	L	H	L	H
Phasianidae	13.5	17.8	16.5	19.3	22.8 ^a	24.1
Columbidae	11.9	15.5	8.7	14.0	14.6	17.9
Corvidae	22.7 ^a	15.5	14.5	10.9	12.2	10.5
Passeriformes	16.7	20.1	20.2	24.6	22.8	30.9
Other birds	7.0	11.5	11.2	9.7	9.1	4.3
Leporidae	21.1 ^b	9.8 ^b	22.4 ^b	10.1 ^b	14.6 ^{a,b}	4.9 ^b
Sciuridae	1.6	6.9	2.5 ^b	7.5 ^b	2.4	6.2
Other prey	5.4	2.9	4.0	3.9	1.6	1.2
N	185	174	401	414	254	162
H'	2.74	2.84	2.76	2.82	2.69	2.54

^a Significantly different from expected frequency when compared with the same habitat in other years.

^b Significantly different from expected frequency when compared with the other habitat in the same year.

and Lalanda 1972, Veiga 1982, Garrigues et al. 1990, Mañosa et al. 1990), but only in some European localities (Sladek 1963, Goszczyński and Pilatoski 1986), and might be correlated with the abundance of ocellated lizards (*Lacerta lepida*) in the Mediterranean regions of the Iberian peninsula.

Game birds, mostly red-legged partridges, was the group most frequently captured and the least variable between samples and seasons, which might be caused by a certain degree of preference or local abundance of that prey. However, even taking into consideration that our methodology may over estimate the frequency of rabbits in the diet, in terms of biomass this was the more important prey species for goshawks in La Segarra especially outside the breeding season. Although rabbits have also been reported as an important prey for goshawks in other areas of Europe (Tinbergen 1936, Sladek 1963, Brüll 1964, Marquis and Newton 1982), only the Iberian localities studied so far shared this characteristic in a consistent geographic pattern.

The different methods used, as well as true seasonal trends, might be partially responsible for the differences between breeding and non-breeding season diet, because smaller or less conspicuous prey might be hard to detect when searching for pluckings outside the nesting season (Opdam et al. 1977). Also, seven of the 10 regularly surveyed pairs outside the breeding season were in the lightly forested area, which might have contributed to an overestimate of the proportion of rabbit in the diet of the whole population at this time of the year. However, the

seasonal trends detected in dietary diversity and average weight of prey are consistent with those found in other European areas (Opdam et al. 1977, Widén 1987). This suggests that goshawk diet composition in La Segarra was largely determined by the diversity and availability of vulnerable prey, which was higher in spring and summer. The lowest proportion of resident and summer birds (Phasianidae, Corvidae and other birds) in the diet were reached in the January–April period, and coincided with their lowest population levels. This was not found for pigeons and passerines, in which the autumn and winter populations may be increased by wintering or migrant birds. The abundance of young birds could be as well a crucial factor determining the importance of different species in the spring and summer diet, and the goshawk would switch from one to another as they become available: from May–July, the total proportion of pigeons and corvids in the diet increased as the proportion of fledgling pigeons and fledgling corvids in the diet increased, whereas the total proportion of passerines decreased as fledgling thrushes (the main passerine group in the diet) decreased. Also, the increase in the consumption of partridges from June–July paralleled the increase in the proportion of young partridges in the diet. Similar importance of young birds and mammals in the diet of goshawks has been reported in other regions (Schnell 1958, Sulkava 1964, Opdam et al. 1977, Wikman and Tarsa 1980, Reynolds and Meslow 1984).

The versatility of feeding by the goshawk was

further emphasized when comparing lightly forested and heavily forested areas. Rabbits and corvids on one hand, and squirrels and pigeons (mainly wood pigeon) on the other, favor farmland and forest habitats respectively, and goshawks took advantage of them differentially in each habitat type. However, the proportion in the diet of other prey types (game birds) did not seem to reflect relative abundance in each environment, which might be a consequence of the unit-sum constraint of proportions (Aebischer and Robertson 1993), or of differences in the vulnerability of these prey between habitats, regardless of their abundance. After the sudden decline on rabbit availability in La Segarra, probably as a consequence of the outcome of the viral haemorrhagic disease (Mañosa 1991), goshawks showed a functional response involving a reduction of rabbit consumption and an increased predation on red-legged partridge. This response, expressed as a proportional change in rabbit consumption, was larger than that observed in golden eagles (*Aquila chrysaetos*; Fernández 1993). In the golden eagle (a rabbit specialist in Mediterranean areas), diet diversity increased following rabbit population crash. This was less in the case of the goshawk, an essentially bird-eating raptor which seems to prey opportunistically on rabbits. The effect on the partridge population of that increase in goshawk predation will depend on the numerical response of goshawk after the rabbit population crash. Further long-term monitoring of breeding densities, breeding success and diet of goshawks and their prey in La Segarra would provide a better understanding of the mechanisms underlying predator-prey interactions in Mediterranean agricultural landscapes.

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THE ANTIPREDATOR VOCALIZATIONS OF ADULT EASTERN SCREECH-OWLS

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ABSTRACT.—Adult eastern screech-owls (*Otus asio*) used six different vocalizations (bounce songs, whinny songs, bark calls, bark-screech calls, screech calls, and bill-claps) during trials in which a human approached nest sites or approached and handled nearly-fledged or recently-fledged young. Bounce songs and whinny songs were uttered more frequently during nest defense trials while bark calls, screech calls and bill-claps were uttered more frequently during trials with young owls. We suggest that bounce and whinny songs serve as low-intensity warnings to mates and nestlings. Bark calls consisted of a single, short duration note and appear to serve as warning calls, informing a mate and young of an approaching predator and informing the predator of a willingness to attack. Screech calls were short duration, high volume calls. Most screech calls were given during flights directed at the predator, and may function as a high-intensity warning call. Bark-screech calls appeared intermediate to bark and screech calls, both in structure and function. Most bill-claps were given during flights directed at the predator, often in conjunction with screech calls. We suggest that the combined vocal signal of screech calls and bill-claps represents the highest-intensity vocal warning directed at potential predators by screech-owls.

KEY WORDS: *eastern screech-owl; vocalizations; antipredator; nest defense; Otus asio.*

Vocalizaciones antidepredadoras de individuos adultos de *Otus asio*

RESUMEN.—Individuos adultos de la especie *Otus asio* usaron seis vocalizaciones diferentes (cantos de bravata, relinchos, llamados de tipo gruñidos o ladridos, mezcla de gruñidos y chillidos, sólo chillidos y golpes de pico) durante ensayos en los que un humano se aproximó a los nidos o aproximó y tomó a los polluelos. Tanto el canto de bravata como los relinchos fueron utilizados con mayor frecuencia durante la defensa del nido, mientras que las demás vocalizaciones fueron frecuentemente utilizadas durante el acercamiento a juveniles. Sugerimos que, tanto la como el relincho, sirven como alertas de baja intensidad para la pareja y los volantones. Los llamados de gruñidos o ladridos, de una simple nota de corta duración, parecen servir para alertar, informando tanto a la pareja como a las crías de la aproximación de un depredador a informando al depredador de su disposición de ataque. Los chillidos son de corta duración, pero son llamados de alto volumen. La mayoría de los chillidos fueron hechos durante vuelos hacia el depredador y podría corresponder a un llamado de alerta de alta intensidad. Los llamados de chillidos y gruñidos parecen estar en una categoría intermedia entre los llamados de gruñidos y los de chillidos, tanto en estructura como en la función. La mayoría de los golpes de pico fueron realizados durante los vuelos hacia el depredador, a menudo mezclados con llamados de chillidos. Sugerimos que esta última combinación de señales vocales representan la alerta de mayor intensidad vocal dirigidas al potencial depredador por parte de *O. asio*.

[Traducción de Ivan Lazo]

The responses of parent birds to an approaching predator may vary considerably, but often include vocalizations, distraction displays, or attacks. Such behaviors may enhance a parent's reproductive suc-

cess but do entail some survival cost (Montgomerie and Weatherhead 1988). The extent of that cost varies with the type of response. Distraction displays, such as dives and attacks, may be relatively expensive and risky (Andersson et al. 1980, Greig-Smith 1980, Curio and Regelman 1985, Knight and Temple 1988). In contrast, vocalizing is neither particularly costly nor risky and, as a result, many parent birds respond to approaching predators by vocalizing (Greig-Smith 1980, Bjerke et al. 1985,

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Table 1. Comparison of the whinny songs and bark calls of male and female eastern screech-owls.

	MALES ^a		FEMALES ^b		COMPARISON OF MALE AND FEMALE VOCALIZATIONS (WILCOXON TEST)	
	MEAN	SE ^c	MEAN	SE ^c	<i>z</i>	<i>P</i>
Whinny songs						
Duration (sec)	1.12	0.02	1.13	0.05	0.18	0.8577
Minimum frequency ^d	684.5	14.0	688.6	31.9	1.30	0.1923
Maximum frequency ^d	1101.5	16.7	1419.4	61.7	4.13	<0.0001
FMA ^e	940.8	15.4	1080.0	32.9	3.89	<0.0001
Bark calls						
Duration (sec)	0.24	0.06	0.25	0.01	1.11	0.2670
Minimum frequency	749.4	10.9	813.5	9.3	4.52	<0.0001
Maximum frequency	1092.8	11.3	1147.6	13.5	2.07	0.0382
FMA	959.4	9.5	1014.3	10.0	3.47	0.0005

^a Eight males gave 80 whinny songs and nine males gave 124 bark calls.
^b Five females gave 35 whinny songs and 136 bark calls.
^c Standard error.
^d All frequency measurements in Hertz.
^e Frequency at maximum amplitude in Hertz.

Veen and Piersma 1986, Knight and Temple 1986, 1988, Weatherhead 1989). Even well-armed parents (i.e., raptors) may respond to potential predators by vocalizing (e.g., Wiklund and Stigh 1983, Andersen 1990).

Adult eastern screech-owls (*Otus asio*) utter a variety of vocalizations in response to potential predators (Sproat 1992, Sproat and Ritchison 1993). We previously examined the nest defense behavior of eastern screech-owls and reported the use of five antipredator vocalizations (Sproat and Ritchison 1993) but did not provide a detailed description of the vocalizations or discuss possible functions. Here we provide such a description and also discuss the possible function(s) of these vocalizations.

METHODS

The vocal responses of male and female eastern screech-owls to potential predators approaching nest sites or young were examined during three breeding seasons (1985, 1990 and 1991) at the Central Kentucky Wildlife Management Area, located 17 km southeast of Richmond, Madison County, Kentucky. A detailed description of methods used during the nest defense trials can be found in Sproat and Ritchison (1993). Briefly, eight pairs of radio-tagged screech-owls (*N* = 4 in 1990 and *N* = 4 in 1991) were tested repetitively while six pairs (*N* = 4 in 1990 and *N* = 2 in 1991) were tested only once. The repetitive pairs were each tested three or four times, with trials conducted at 12–14 d intervals during the approximately eight-week nesting cycle. Two people were involved in each trial, one acting as an observer and the other as the predator. During

each trial, the predator spent 8 min at a point 8 m in front of the nest tree, four min at the base of the nest tree, 4 min about halfway between the ground and the cavity (using a ladder), and a final 4 min at the initial location in front of the nest tree.

To obtain additional recordings, we also examined the responses of eight pairs of screech-owls (three in 1985, three in 1990, and two in 1991) to humans just prior to or after fledging of their young. Pairs tested in 1990 and 1991 had also been used for the nest defense trials while those tested in 1985 had not been tested previously. Further, only those pairs tested in 1990 and 1991 were fitted with radiotransmitters. During these nestling/fledgling trials, young were removed from nest cavities or roost sites, tethered to a branch, and approached and handled by a human. These trials varied in duration and during each trial an attempt was made to record all vocalizations uttered by the adults. Because paired owls were sometimes in close proximity during these trials, we were not always able to determine whether the male or female was vocalizing. We also attempted to determine the number of dives (any break in horizontal flight directed at the predator) made by each member of the pair.

During all trials we noted the number and type of vocalizations uttered by parent owls. Vocalizations were recorded by the person acting as the predator using a Uher 4000 Report Monitor tape recorder with a Dan Gibson parabolic microphone. All vocalizations recorded on tape were subsequently analyzed using a Kay Elemetrics Corp. Sonagraph (Model 5500). For each vocalization we determined duration, maximum frequency, minimum frequency, frequency at maximum amplitude (FMA), and, for bounce songs, the number of notes per song.

Multiple comparisons were made using a one-way ANOVA applied to ranks (equivalent to a Kruskal-Wallis

test; SAS Institute 1985) while paired comparisons were made using Wilcoxon tests (SAS Institute 1985). Chi-square tests were used to test for non-random distributions. All values are presented as mean \pm standard error.

RESULTS

Eastern screech-owls uttered six different vocalizations during the trials: bounce songs, whinny songs, bark calls, bark-screech calls, screech calls, and bill-claps (Fig. 1). Male screech-owls gave all of these vocalizations while females gave all except bounce songs.

Description of Vocalizations. The bounce songs of male screech-owls ($N = 39$ songs by seven individuals) averaged 1.92 ± 0.06 sec in duration and consisted of an average of 25.33 ± 1.03 notes. The mean frequency at maximum amplitude (FMA) was 620.0 ± 6.1 Hz. The bounce songs of males exhibited significant individual variation in number of notes per song ($F_{4,29} = 4.07$, $P = 0.0097$), maximum frequency ($F_{4,29} = 4.13$, $P = 0.0009$), minimum frequency ($F_{4,29} = 4.07$, $P < 0.0001$), and FMA ($F_{4,29} = 5.96$, $P = 0.0013$) but not in duration ($F_{4,29} = 1.52$, $P = 0.222$).

The whinny songs of male ($N = 8$) and female ($N = 6$) screech-owls differed significantly in maximum frequency and FMA but not in duration or minimum frequency (Table 1). Among males, whinny songs differed significantly in duration ($F_{7,72} = 3.95$, $P = 0.001$), maximum ($F_{7,72} = 34.08$, $P < 0.0001$) and minimum ($F_{7,72} = 21.65$, $P < 0.0001$) frequency, and FMA ($F_{7,72} = 34.79$, $P < 0.0001$). Similarly, among females, whinny songs differed significantly in duration ($F_{5,29} = 6.74$, $P = 0.0003$), maximum ($F_{5,29} = 41.65$, $P < 0.0001$) and minimum ($F_{5,29} = 6.71$, $P = 0.0003$) frequency, and FMA ($F_{5,29} = 25.56$, $P < 0.0001$).

Bark calls consisted of a single note that typically exhibited a gradual decline in frequency (Fig. 1). The barks of female screech-owls were significantly higher in frequency than those of males (Table 1). Among males, bark calls exhibited significant individual variation in duration ($F_{9,115} = 4.61$, $P < 0.0001$), maximum ($F_{9,115} = 5.19$, $P < 0.0001$) and minimum ($F_{9,115} = 4.65$, $P < 0.0001$) frequency, and FMA ($F_{9,115} = 5.83$, $P < 0.0001$). Similarly, among females, bark calls exhibited significant individual variation in duration ($F_{4,131} = 5.82$, $P = 0.0002$), maximum ($F_{4,131} = 6.46$, $P < 0.0001$) and minimum ($F_{4,131} = 4.56$, $P = 0.0018$) frequency, and FMA ($F_{4,131} = 6.06$, $P = 0.0002$).

Bark calls were sometimes given in bouts of two

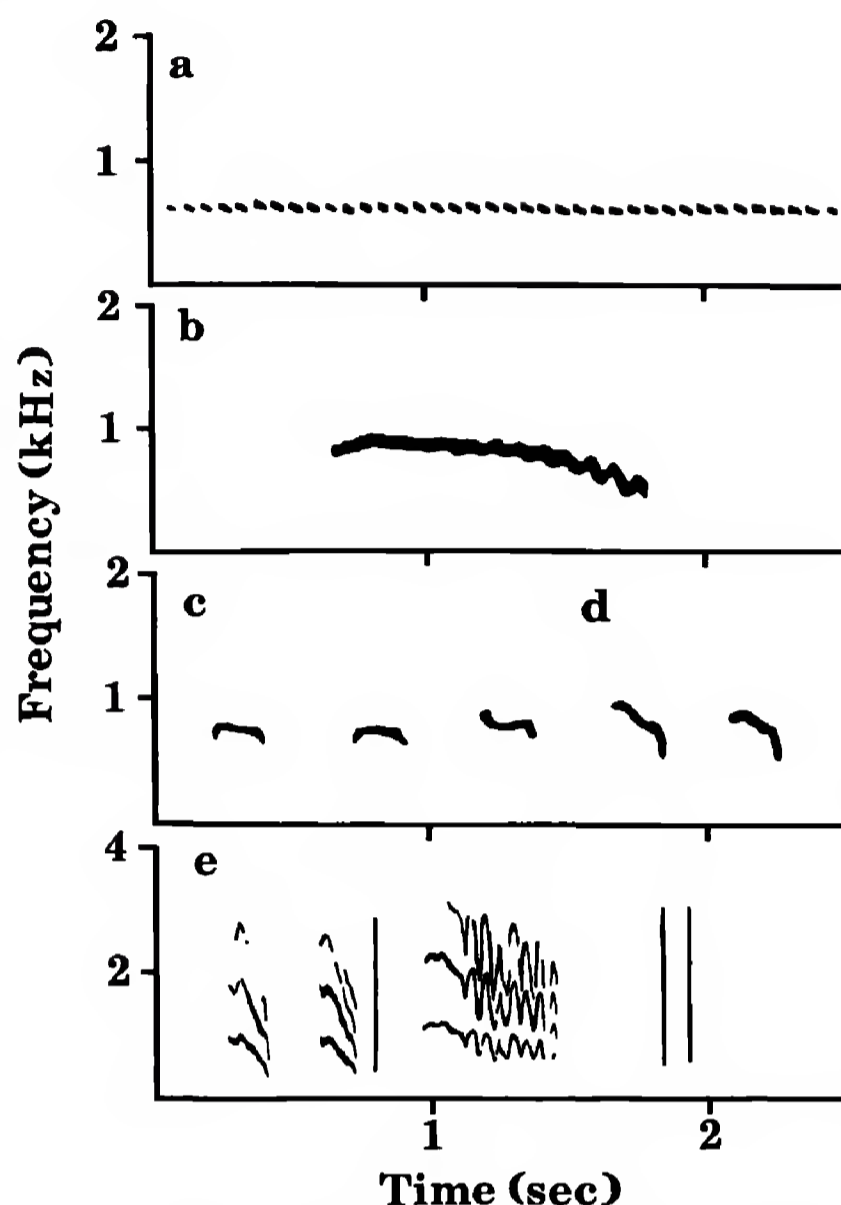


Figure 1. The antipredator vocalizations of eastern screech-owls. (a) bounce song, (b) whinny song, (c) three bark calls, (d) two bark-screech calls, and (e) two screech calls followed by a single bill-clap plus a screech call exhibiting frequency modulation followed by two bill-claps

or more (with a bout defined as a series of the same calls with intercall intervals of 30 sec or less). The mean number of bark calls per bout ($N = 71$ bouts by at least 18 individuals) was 6.42 ± 1.01 . Females ($N = 6$) gave significantly ($z = 3.21$, $P = 0.0013$) more bark calls per bout than did males ($N = 8$), with males averaging 3.87 ± 0.83 calls per bout and females averaging 5.96 ± 0.86 calls per bout.

Bark-screech calls were uttered by one or both members of one pair of screech-owls during a nestling/fledgling trial, and the characteristics of these calls were intermediate to those of bark and screech calls. Bark-screech calls ($N = 19$) averaged 0.21 ± 0.01 sec in duration and had a mean FMA of 793.2 ± 11.5 Hz. These calls exhibited a sharp drop in frequency, descending from a mean high frequency

of 943.2 ± 36.3 Hz to a mean low frequency of 523.7 ± 45.4 Hz.

Screech calls were high volume calls consisting of a single note exhibiting a rapid drop in frequency (Fig. 1). Screech calls sometimes ended with a series of frequency modulations (Fig. 1). Most screech calls were given by owls in flight, often during dives. Screech calls ($N = 53$) averaged 0.25 ± 0.02 sec in duration and had a mean FMA of 884.7 ± 20.5 Hz. These calls descended from a mean high frequency of 1217.1 ± 24.6 Hz to a mean low frequency of 443.2 ± 17.7 Hz. We were able to positively identify only three of the owls (two females and one male) that uttered these calls and, therefore, could not compare the screech calls of males and females.

Bill-claps produced short duration sounds ($\bar{x} = 0.02 \pm 0.0004$ sec; $N = 46$ by at least four individuals) that covered a wide range of frequencies (Fig. 1). Although most bill-claps were given immediately before or after bark calls ($N = 12$) or screech calls ($N = 24$), three screech-owls gave only bill-claps during dives. When given with other calls, bill-claps were given an average of 0.25 ± 0.15 sec ($N = 2$) before bark calls, 0.31 ± 0.08 sec ($N = 5$) before screech calls, 1.36 ± 0.85 sec ($N = 7$) after bark calls, and 0.17 ± 0.03 sec ($N = 13$) after screech calls. No significant differences were found between the bill-claps of males and females (Wilcoxon tests, $P > 0.05$). Bill-claps were often given in bouts of two or more. The mean number of bill-claps per bout was 1.63 ± 0.13 ($N = 27$ bouts by at least four individuals) and the mean duration of these bouts was 0.16 ± 0.03 sec.

Vocal Responses During Nest Defense and Nestling/Fledgling Trials. Few vocalizations were uttered during the incubation stage ($N = 19$ trials). Female screech-owls ($N = 2$) vocalized during two trials, with one female giving one whinny song and the other 15 whinny songs. Males ($N = 5$) vocalized during five trials, with one male giving one whinny song and five bounce songs, a second male giving one bark, and three males giving bounce songs (1, 1, and 16, respectively).

Screech-owls vocalized during 14 of 17 trials conducted during the nestling stage. Bark calls ($N = 103$ by eight males and two females during eight trials) and whinny songs ($N = 94$ by eight males and four females during eight trials) were the most frequently used vocalizations during the nestling stage. Screech-owls gave few bounce songs ($N = 11$ by three males) and screech calls ($N = 5$ by two

males and one female) and no bill-claps. Male screech-owls were more vocal than females, with only males vocalizing during seven trials and both the male and female vocalizing during seven additional trials. In addition, vocalizing males gave more calls, averaging 11.4 bark calls ($N = 8$ males) and 7.8 whinny songs ($N = 8$ males). Vocalizing females averaged six bark calls ($N = 2$ females) and 4.5 whinny songs ($N = 4$ females).

Vocalizations were uttered by adult male and female screech-owls during seven of eight nestling/fledgling trials. Screech-owls used all six vocalizations during these trials, with bark calls given most frequently. During three of the seven nestling/fledgling trials in which adult screech-owls uttered vocalizations, we were unable to positively identify the source (i.e., adult male or adult female) of some or all of the vocalizations. For the remaining four trials, we found that female screech-owls uttered significantly more ($\chi^2 = 16.2$, $df = 3$, $P = 0.001$) bark calls per trial than did males, with females averaging 31 ± 13.3 bark calls and males 8.3 ± 5.9 bark calls.

Among those pairs tested during both types of trials (nest defense and nestling/fledgling), the use of vocalizations during the two trials differed significantly ($\chi^2 = 47.6$, $df = 4$, $P < 0.0001$). Bark calls, screech calls, and bill-claps were used more frequently during the nestling/fledgling trials while bounce songs and whinny songs were used more frequently during the nest defense trials.

DISCUSSION

Eastern screech-owls in our study uttered bounce and whinny songs in an antipredator context; however, these songs are also used in other contexts (Ritchison et al. 1988, Klatt and Ritchison 1993). Bounce songs given by male screech-owls in our study averaged 25.3 notes. By comparison, bounce songs given in response to playback averaged 32.3 notes (Cavanagh and Ritchison 1987) while those uttered during duets averaged 58.4 notes (Klatt and Ritchison 1993). Thus, our results support the hypothesis that the message conveyed by bounce songs varies with song length—shorter songs conveying increasing levels of aggression (Klatt and Ritchison 1993) or perhaps anxiety. Most bounce songs were given during the incubation period when screech-owls exhibited little nest-defense activity (Sproat and Ritchison 1993). These results suggest that bounce songs were probably directed by males toward their

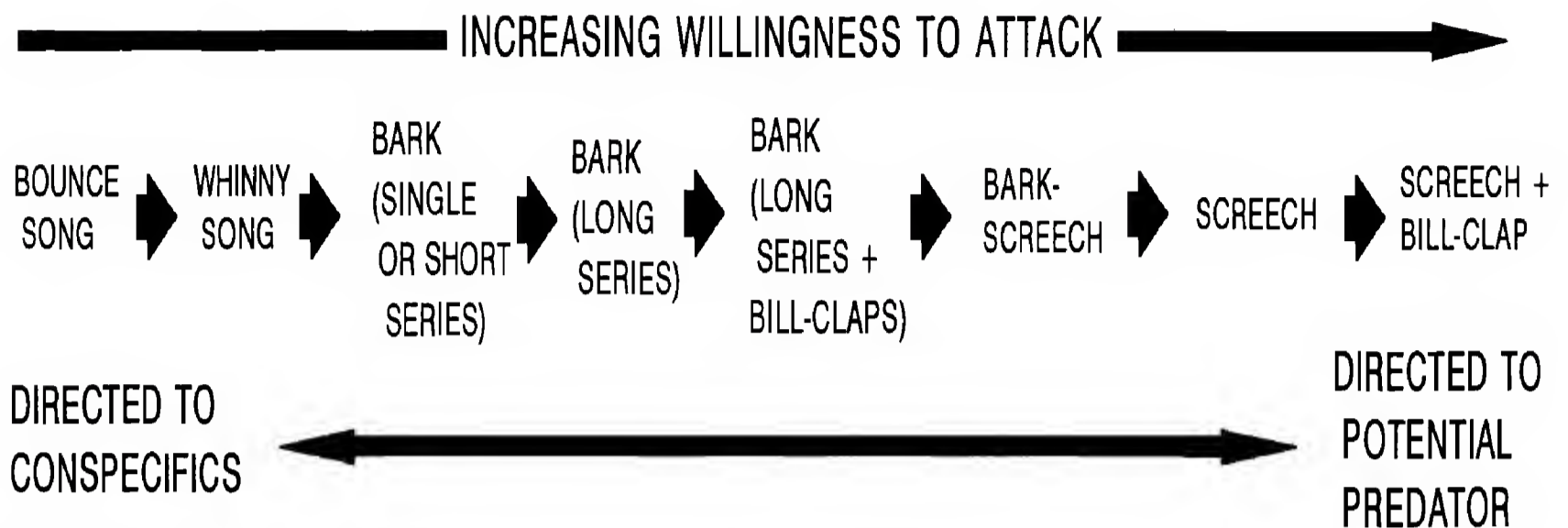


Figure 2. A possible antipredator communication system of adult eastern screech-owls.

incubating mate and served as a low-level warning (Fig. 2).

Screech-owls responded with significantly greater intensity during the nestling stage than during incubation (Sproat and Ritchison 1993), and most whinny songs were given during the nestling stage. Whinny songs are also given with greater volume than bounce songs (Ritchison et al. 1988). This increased volume, plus the association with other antipredator behaviors (e.g., flights and dives), suggests that whinny songs serve as a higher-level warning to mates and nestlings (Fig. 2). The characteristics of whinny songs also make a calling bird relatively easy to locate (Ritchison et al. 1988), suggesting that they may also serve to distract potential predators. Selection should favor the use of easily locatable calls as distraction displays when the caller's position must be revealed (Greig-Smith 1980). Vocalizations that apparently serve to distract predators have been reported in several other species (Greig-Smith 1980, East 1981, Andersen 1990).

Screech-owls in our study also uttered bark calls, bark-screech calls, screech calls, and bill-claps. These calls have been reported previously (Marshall 1967, Walker 1974, Voous 1988, Torre 1990) and are apparently uttered only in aggressive or defensive contexts (Torre 1990). Other species of owls utter similar calls in aggressive contexts. For example, boreal owls (*Aegolius funereus*) utter screech calls when the nest or fledged young are approached by potential predators (Meehan 1980). Bark-like calls have been reported in snowy owls (*Nyctea scandiaca*), little owls (*Athene noctua*), barred owls (*Strix varia*), spotted owls (*S. occidentalis*), and boreal owls (Voous 1988). Bill-claps have also been reported in several

species of owls, and are generally uttered in aggressive (including nest protection) or defensive contexts (Johnsgard 1988).

Bark calls were uttered by male and female screech-owls during the nestling stage and, especially, during the nestling/fledgling trials. Our results indicate that bark calls serve to warn a mate and young that a predator is approaching. Kelso (1938:248) reported that when two juvenile screech-owls heard bark calls "... they crouched flat ... and feigned death." Calls with a similar function have been reported in other species (e.g., Greig-Smith 1980, Knight and Temple 1986, 1988, Andersen 1990).

Screech-owls sometimes gave long series of bark calls, particularly during the nestling/fledgling trials. Previous studies suggest that a single call, or a short series of calls, may be sufficient to convey a warning of danger to a mate or young and, further, that a long series of calls are more likely directed at the predator (Powell 1974, Greig-Smith 1980). Our results support this hypothesis. Screech-owls gave relatively short bouts of bark calls during the nest defense trials and these bouts preceded a dive only once, suggesting that the calls were directed at a mate or young. In contrast, the longer series of barks given during the nestling/fledgling trials were often followed by screech calls and dives, suggesting that the calls warn a predator of a screech-owl's increasing willingness to attack (Fig. 2).

Most screech calls were given by screech-owls during flights at the predator, mainly during the nestling/fledgling trials when young were being handled. Kelso (1938:248) observed that screech-owls gave screech calls "... when a person or large animal comes near the young either while they are

in or out of the nest. It is usually given as the male swoops at the intruder's head. . . ." The relatively high volume of these calls and the tendency to utter them close to the predator indicate that the calls are directed at the predator and serve as a high-intensity warning (Fig. 2). Bark-screech calls were also given during the nestling/fledgling trials and appeared intermediate to bark calls and screech calls, both in terms of structure and function (Fig. 2).

All bill-claps were given during the nestling/fledgling trials, mainly during flights at the potential predator (often in conjunction with screech calls). As with screech calls, the association of bill-claps with flights at the predator indicates that they are directed at the predator and serve as a high-intensity warning. The combined vocal signal of screech calls and bill-claps may represent the highest-intensity vocal warning given by screech-owls (Fig. 2).

Male screech-owls vocalized more than females during our nest defense trials. Similarly, Sproat and Ritchison (1993) found that male screech-owls defended young in the nest more vigorously than did females. However, female screech-owls vocalized more than males during our nestling/fledgling trials and, in at least two pairs, females made more flights at the predator. Such results suggest that the intensity of defense by female screech-owls may increase when a predator poses a greater threat (i.e., is closer) to the offspring and support the hypothesis that the location of a predator relative to the nest (or fledged young) may influence the defense behavior of male and female raptors that exhibit reversed sexual dimorphism (Sproat and Ritchison 1993).

In summary, eastern screech-owls use several vocalizations in an antipredator context and we suggest that these vocalizations represent a graded system of communication (Fig. 2). Similar graded systems have been reported in other species (Morton and Shalter 1977, Miller 1979, Veen and Piersma 1986, Armstrong 1992), and such systems permit more precise communication because individuals are able to communicate subtle variations in motivation (Morton 1977).

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BEHAVIOR AND ACTIVITY OF REHABILITATED BUZZARDS (*Buteo buteo*) RELEASED IN NORTHERN ITALY

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ABSTRACT.—The behavior and habitat hunting of 16 rehabilitated common buzzards (*Buteo buteo*) released in northern Italy were analyzed. The buzzards were released individually in different seasons, and their activity was recorded continuously for at least the first 3 d after release and intermittently thereafter until they dispersed from the release site. The birds remained in the surrounding area for more than 100 d, showing a progressive acclimation to the new environment. The released buzzards interacted frequently with wild territorial conspecifics and were attacked by several species of corvids, especially the hooded crow (*Corvus corone*). Nevertheless, such interactions were not the direct cause of dispersal. Some birds defended a territory adjacent to or inside that of a wild buzzard. Prey capture was almost normal, although certainly underestimated. Small mammals and reptiles were most often caught. Although the area chosen for this study had high human population, this was not a major source of interference with the releases. Thus, the buzzards appeared to be able to cope with their new environment being minimally influenced by having been in captivity.

KEY WORDS: *hawks; Buteo buteo; behavior; captivity; dispersal; rehabilitation; behavioral ecology.*

Comportamiento y actividad de los *Buteo buteo* rehabilitados y deydados en libertad en el norte de Italia

RESUMEN.—Se analizó la conducta y el habitat de caza de 16 individuos rehabilitados de la especie *Buteo buteo* liberados en el norte de Italia. Los individuos de *B. buteo* fueron liberados en el área de estudio individualmente y en diferentes estaciones; su actividad fue registrada continuamente por al menos tres días después de su liberación e intermitentemente hasta el momento de abandonar el sitio de liberación. Las aves permanecieron en los alrededores del área por más de 100 días, mostrando una progresiva aclimatación al nuevo ambiente. Los individuos liberados interactuaban frecuentemente con conespecificos territoriales silvestres y fueron atacados por varias especies de cóvidos, especialmente *Corvus corone*. Sin embargo, tales interacciones no fueron la causa directa de su dispersión. Algunas aves defendieron territorios vecinos o al interior de los defendidos por individuos silvestres. La captura de presa fue casi normal, aunque ciertamente subestimada. Tanto pequeños mamíferos como reptiles fueron a menudo capturados. Aunque las áreas escogidas para este estudio tenían una alta población humana, este factor no constituyó una gran fuente de interferencias sobre las liberaciones. En síntesis, *B. buteo* parece ser capaz de insertarse en su nuevo medambiente siendo escasamente influenciado por su cautividad.

[Traducción de Ivan Lazo]

Several programs for the rehabilitation of raptors have been developed in recent years by institutions devoted to the protection of birds. Standard procedures for raptor rehabilitation have been developed for several species (Nelson 1977, Llewellyn and Brain 1983, Pendleton et al. 1987, Weaver and Cade 1991) as well as the techniques for successful release (Sherrod et al. 1982, Llewellyn 1991). Nevertheless, the adaptation of birds back into the natural habitat is

still neglected. In fact, it is almost impossible to get information of the fate of released birds from the literature, because most data refer to survival rate and recovery distance from the release site (Servheen and English 1979, Duke et al. 1981, Ingram 1983, Hamilton et al. 1988). Moreover, little precise information has been compiled on the behavior of individuals after release.

The objective of this study was to fill that gap, investigating in detail the behavior, activity, and intra- and interspecific interactions in a group of common buzzards (*Buteo buteo*) immediately after release following rehabilitation until they dispersed

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from the area. Such an investigation is likely to be of interest to raptor rehabilitators (Meyers and Miller 1992).

METHODS

The buzzards used in this study were all wild birds, housed temporarily for rehabilitation at the Raptor Rehabilitation Centre (RRC) managed by the Italian Society for the Protection of Birds (LIPU) near Parma. They all originated in northern or central Italy within 100–200 km of the release area. When released the birds were all in perfect physical condition and flying fitness, and were chosen randomly among those ready for releasing. Those possibly imprinted to humans were not considered.

A total of 16 buzzards were studied. Six were adult (two males and four females) and 10 were sub-adults (five males and five females). They were released near the end of each season, from April 1990 to November 1991. Five were studied between winter and spring, four between spring and summer, three between summer and autumn, and four between autumn and winter. Thus, we avoided the most stressful climatic conditions that occur in January–February and in July–August (Kostrzewa and Kostrzewa 1991). The duration in captivity was variable, ranging from a few days to several months, depending on the seriousness of the injury or illness. The mean duration for nine buzzards was 295.5 ± 109.2 d. We did not know the period for the other five, but it was certainly within the same range.

The release site was located within a waterfowl sanctuary managed by LIPU about 15 km north of Parma and 5 km from the Po River. The area is flat and without extensive woodlands but with a high human population density. The site was chosen because of the necessity to observe closely and track the buzzard behavior precisely, even for long distances if necessary. Wild buzzards are regularly present particularly during winter. Several taxa of invertebrates and terrestrial vertebrates offered an easy and variable food source.

The area surrounding the release site contained several biotopes, with rather differing vegetal cover. The habitat types were evaluated using the method described by Emlen (1956). Several watercourses—the Parma River and several streams—run within the study area. Most of the trees are concentrated along them.

The buzzards were released individually between 0900–1500 H on days without precipitation. Beforehand they were kept on location in an outdoor aviary for 1–2 wk in order for them to habituate to the environment. A radiotag (9 g two stage, BIOTRACK, Wareham, U.K.) was attached some hours before release (Kenward 1987, White and Garrott 1990).

The buzzards were followed virtually continuously from dawn to dusk each day if weather permitted for the first 3 d after release, hereafter referred as “days 1–3.” If a bird did not leave the area, it was subsequently monitored intermittently with the same schedule at 1–4 d intervals, until the bird disappeared from the surroundings. That period, including the first 3 d, is hereafter indicated as “all-days.” Observations were carried out using 8× binoculars and a 10–40× zoom spotting scope.

The daylight period was equally divided into three sections that were variable during the year based upon the photoperiod. The proportion of time spent in each habitat for each one-third of the daylight period and in every season was arcsin transformed for comparison. The exact time of sunrise and sunset for the geographical coordinates of the area were calculated every 2 wk. The days after release were counted considering the day of release as day one. The days of the year were indicated considering the spring equinox as day zero.

We used the Mann-Whitney U-test to compare means, the Kruskal-Wallis one-way ANOVA (Siegel 1956) to evaluate time durations between seasons or between thirds of the day, the Spearman rank correlation to ascertain possible correlations, and the Chi-square test to compare frequencies. The means are given \pm SE, and the probability is always given as two-tailed.

RESULTS

Most buzzards did not disappear quickly from the release site in 426.6 hr of observation (Table 1). The area used by the birds was about 2730 ha in size, almost centered around the release site. One-half of the sampled buzzards left the study area within three days. Three departed within a few hours and one on day three. This occurred in early spring and autumn.

Mortality. Three buzzards died in the study area by electrocution after perching on medium-tension pylons which are widely distributed in the plains of Italy, and unfortunately are a serious problem for other species too. One bird died of a gunshot wound received during the night or at dawn before we started our observation session, and another died in spring for unknown reasons during a late snowfall. Finally, one buzzard was recaptured close to starvation.

Habitat Use. Habitat types within the study area were small. Their distribution was almost regular, and the buzzards moved very easily from one habitat to another. We found great individual variability in habitat use ($H = 31.79$, $N = 450$, $P < 0.001$, measured as minutes spent by each bird in each habitat). Birds that changed habitat frequently had been kept in captivity for the least time ($Z = 2.18$, $N = 279$, $P < 0.05$). During winter, buzzards stayed in one habitat longer than in other seasons, both during days 1–3 ($H = 10.28$, $N = 390$, $P < 0.05$) and in all-days ($H = 17.58$, $N = 485$, $P < 0.001$).

The buzzards remained longer in open habitats than in areas with thick vegetation in every period considered (Kostrzewa 1989). The tendency to explore different habitats immediately after release, i.e., the minutes spent in each habitat before moving to another one, decreased with time ($r_s = 0.10$, $N =$

Table 1. The history of common buzzards released following rehabilitation near Parma, Italy.

BUZZARD IDENTIFI- CATION CODE	SEX, AGE	DATE OF RELEASE	DAYS REMAINING WITHIN THE STUDY AREA	DURATION OF OBSERVATION (hr)	CAUSE OF OBSERVATION END
VR-340	M, JU	25 Oct 1990	1	1.5	Abandonment ^a
AV-670	F, AD	6 Dec 1990	1	2.8	Abandonment ^a
RN-700	F, JU	27 Mar 1991	1	5.2	Abandonment ^a
V-525	F, AD	11 Apr 1990	3	17.4	Abandonment ^a
O-790	F, JU	15 Jun 1990	4	27.0	Abandonment ^a
VA-425	F, JU	19 Jun 1991	4	25.7	Abandonment ^a
NM-920	M, AD	11 Sep 1991	4	28.2	Abandonment ^a
VN-355	M, JU	13 Apr 1991	7	30.4	Death
RN-670	F, JU	17 Nov 1990	11	37.7	Death
VP-960	M, JU	20 Sep 1991	13	29.0	Death
AN-690	F, AD	16 Mar 1991	14	45.2	Abandonment ^a
B-355	F, JU	30 Apr 1991	18	31.3	Abandonment ^a
A-260	M, JU	9 Jun 1990	29	33.9	Abandonment ^a
GM-440	M, AD	3 Nov 1990	39	46.5	Recapture
RS-1150	F, AD	15 Sep 1991	65	34.7	Abandonment ^a
RA-450	F, AD	23 Jun 1991	103	30.2	Abandonment ^a

^a Buzzard left the release area.

485, $P < 0.05$). Habitats with trees were used most (74.8% of time), particularly tree rows (55.9%). The time spent in such habitats was inversely correlated with tree distance ($r_s = -0.12$, $N = 310$, $P < 0.05$). The birds preferred those areas in spring, particularly the “irregular” woods ($H = 11.29$, $N = 147$, $P < 0.02$) and poplar plantations ($H = 11.02$, $N = 147$, $P < 0.02$), while in summer they stayed mostly in woods with trees in rows ($H = 12.54$, $N = 146$, $P < 0.01$). Such a preference changed dramatically in autumn and winter, when the birds chose principally open/cultivated areas ($H = 20.55$, $N = 147$, $P < 0.001$). In contrast, they appeared to avoid the vicinity of buildings or other areas where human presence was evident. Only six birds frequented such areas, perching close to human settlements and spending no more than 20% of the observation period there. We found no relationship between time of day and habitat preference. The birds remaining for a long time within the study area were also able to occupy a territory adjacent to or within a territory defended by a wild conspecific, but behaved as subordinate to the latter.

Perching Sites. The buzzards perched most frequently in tree branches, but also often used pylons, poles, or simply stood on the ground. In spring ($N = 148$) they perched most often on poplars (*Populus*

spp.; $\chi^2_{(1)} = 111.90$, $P < 0.001$) and willows (*Salix alba*; $\chi^2_{(1)} = 12.99$, $P < 0.001$), while in summer ($N = 221$) they rested in oaks (*Quercus* spp.; $\chi^2_{(1)} = 18.11$, $P < 0.001$) and again in poplars ($\chi^2_{(1)} = 42.75$, $P < 0.001$) and willows ($\chi^2_{(1)} = 15.02$, $P < 0.001$). In autumn ($N = 237$) they preferred open habitats and either perched on pylons ($\chi^2_{(1)} = 21.72$, $P < 0.001$), poplars ($\chi^2_{(1)} = 27.16$, $P < 0.001$) or descended to the ground, but in winter ($N = 46$) they returned to a preference for trees, again principally poplars ($\chi^2_{(1)} = 40.45$, $P < 0.001$). The perching duration was unaffected by the type of perching site and averaged 30.70 ± 1.22 min ($N = 652$).

Perch height was negatively correlated with the perching duration in both days 1–3 ($r_s = -0.10$, $N = 486$, $P < 0.05$) and in subsequent time periods ($r_s = -0.09$, $N = 652$, $P < 0.02$). Height was strongly influenced ($H = 37.14$, $N = 652$, $P < 0.001$) by season in either period ranging from 5.26 ± 0.26 m (all-days) in spring to 3.27 ± 0.17 m (all-days) in summer and in winter.

Flight Performance. The buzzards flew some distance away immediately after release, but remained within a range of 400–5000 m. The distance from the release site increased progressively to 1295.0 ± 217.4 m on day three. These values were greatly affected by season ($H = 18.25$, $N = 551$, $P < 0.001$),

Table 2. Some parameters of flapping or gliding flights and soaring for each released buzzard. (It was not possible to ascertain the actual height of all flights.)

BUZZARD IDENTIFI- CATION CODE	TOTAL NO. OF FLIGHTS	MEAN NO. OF MINUTES BETWEEN TWO FLIGHTS	MEAN NO. OF HOURS BETWEEN TWO SOARING FLIGHTS	MEAN (\pm SE) HEIGHT (m) OF FLIGHT (<i>N</i>)	MEAN (\pm SE) LENGTH (m) OF FLIGHT (<i>N</i>)
AV-670	6	28.3	—	11.5 \pm 1.5 (2)	441.7 \pm 141.8 (6)
RN-700	8	38.8	5.167	—	491.9 \pm 204.6 (8)
VR-340	3	30.0	1.5	—	150.0 \pm 57.7 (3)
V-525	11	95.0	8.733	75.0 \pm 0.0 (2)	336.4 \pm 134.7 (11)
O-790	25	64.8	—	—	173.0 \pm 17.8 (25)
GM-440	51	49.1	46.633	—	187.4 \pm 18.2 (51)
NM-920	48	35.2	28.167	9.1 \pm 1.9 (26)	176.6 \pm 17.6 (48)
VA-425	45	34.2	—	8.2 \pm 0.7 (26)	161.1 \pm 14.9 (45)
VN-355	76	27.2	15.217	14.8 \pm 2.8 (29)	185.0 \pm 20.1 (76)
RN-670	90	24.8	—	—	186.7 \pm 18.3 (90)
AN-690	54	50.2	—	18.5 \pm 11.5 (52)	160.6 \pm 15.0 (54)
VP-960	47	37.0	5.793	18.3 \pm 7.1 (19)	281.4 \pm 41.9 (47)
B-355	42	25.4	7.829	22.1 \pm 5.1 (16)	245.8 \pm 37.7 (42)
A-260	62	33.4	11.305	—	219.4 \pm 22.1 (62)
RS-1150	73	28.5	34.683	7.5 \pm 1.4 (51)	186.3 \pm 20.7 (73)
RA-450	51	35.5	30.183	7.0 \pm 0.9 (43)	132.8 \pm 12.1 (51)

with longer distances in autumn (1043 ± 206 m) and shorter in winter (536 ± 93 m). The time of day did not have any influence.

Most flights involved flapping and gliding with soaring being recorded only at the beginning of spring and autumn. The frequency of flights was highly variable between individuals ($H = 25.11$, $N = 126$, $P < 0.05$), with intervals between two flights ranging from 24.8–95.0 min/bird (Table 2). High frequency of flights was associated with short rehabilitation period ($Z = 2.65$, $N = 11$, $P < 0.01$). The longest flights were in autumn and spring (221.7 ± 14.5 m [$N = 218$] and 223.3 ± 15.0 m [$N = 234$], respectively, in all-days), showing a significant difference among seasons ($H = 12.46$, $N = 692$, $P < 0.01$ in all-days). Flight length increased with distance from release site ($r_s = 0.13$, $N = 692$, $P < 0.001$). Flight height and length were positively correlated ($r_s = 0.31$, $N = 219$, $P < 0.001$).

Predatory Behavior. We recorded 92 predation attempts, 55 of which occurred during days 1–3. Twelve birds out of the 16 studied attempted to catch prey at least once (7.67 ± 2.13 attempts/bird), with much individual variation (one attempt every 1.3 hr to one every 33.9 hr). The four buzzards that died or were recaptured had higher mean frequencies than the surviving birds (one attempt every $2.7 \pm$

0.5 hr vs. one attempt every 17.0 ± 4.1 hr, $Z = 2.12$, $N = 12$, $P < 0.05$). More attempts were recorded during autumn ($N = 43$, one attempt every 2.9 hr) and spring ($N = 32$, one attempt every 4.1 hr) than in winter ($N = 3$, occurring every 12.5 hr). The interval between two prey capture attempts was very variable ($H = 20.09$, $N = 48$, $P < 0.05$). Moreover, the frequency of the attempts increased in relation to days after release ($r_s = 0.35$, $N = 48$, $P < 0.05$).

Buzzards generally hunted from perches (87.0% of total attempts). Only 12 hunts were performed by walking or standing on the ground and only three birds displayed these patterns. Range of prey taken was variable, being mainly comprised of mammals, reptiles, and insects. Although the common buzzard is well able to capture birds (Tubbs 1974), these were not included in our hunting observations in contrast to observations by Lovari (1974). When hunting from perches, buzzards started from a mean height of 4.36 ± 0.26 m. Neither the substrate nor the outcome were related to the height. The quarry was caught at a mean distance of 13.06 ± 1.11 m from the perch (range 2–60 m).

The predation angle, i.e., the angle between the vertical from the perch to the ground and the path from the perch to the prey, supposing a linear glide, covered a wide range (0–85°). This angle was af-

fects by habitat substrate during days 1–3 ($H = 9.92$, $N = 50$, $P < 0.05$). Uncultivated and grass fields accounted for the highest percentage of successful attempts ($N = 10$). Banks of watercourses accounted for 42.9% of uncertain successes ($N = 14$), but the percentage of success related to the grass fields was only 7.1%. Uncultivated or plowed fields produced intermediate results. Unsuccessful attempts ($N = 26$) were mainly recorded in grass fields (38.4%), watercourse banks (34.6%), and plowed fields (19.2%).

The season strongly influenced both the type of perch used for predation attempts ($\chi^2_{(3)} = 42.65$, $P < 0.001$) and the type of habitat substrate where the attempt was performed ($\chi^2_{(3)} = 8.61$, $P < 0.05$). In fact, buzzards preferred to hunt from rows of trees in spring ($P < 0.001$) and from pylons in autumn ($P < 0.001$). Most predation attempts occurred on the grass fields during the cold season.

Interactions with Conspecifics and Other Bird Species. A total of 29 interactions with resident wild buzzards was recorded involving five birds out of the 16 released. Most interactions occurred in summer and autumn (24.1% and 62.1%, respectively; cf. Kozłowska 1991), and we did not record any interaction in winter. Such interactions occurred soon after release; in fact, approximately one-half occurred in days 1–3. The interval between two interactions decreased markedly with days ($r_s = -0.56$, $N = 20$, $P < 0.05$), reaching the maximum value between day 10–30 post-release. The interactions occurred mostly when the released buzzard was perched and were rather variable in duration (range: 5 sec–35 min.), and negatively correlated with perch height ($r_s = -0.66$, $N = 15$, $P < 0.05$). An interaction between two soaring birds was recorded only once. Vocalizations were very frequent during interactions, as observed also by Tubbs (1974).

Wild buzzards attacked first in 55.1% of interactions and the released bird attacked first only in 13.7% of times. Fighting, although of short duration, occurred in 6.8% of observations. In these cases neither buzzard showed a tendency to leave. Attacks by the released buzzard never occurred on day one. Released buzzards that interacted with wild ones scored higher in predation frequency than those not interacting ($Z = 2.11$, $N = 12$, $P < 0.05$). The three birds that interacted most frequently eventually died or were recaptured.

The buzzards in this study interacted with several corvid species much more frequently than with con-

specifics: 317 interactions involving the hooded crow (*Corvus corone*), 63 involved the magpie (*Pica pica*), and 50 the jay (*Garrulus glandarius*). The mean frequency of interaction with the hooded crow was highest in spring and lowest in autumn. The interactions with the magpie were most frequent in autumn and very rare in winter, and those with the jay were rare in winter but similar in the other seasons. Interactions without regard to the bird species most often occurred among rows of trees, ranging from 92.0% for jays to 54.6% for hooded crow. The latter species also frequently mobbed buzzards in open areas (27.4%) and in other types of woods (17.2%). The number of mobbing individuals was highly variable with the maximum by the hooded crow (up to 12 birds and up to eight in the magpie and three in the jay). The corvids involved in mobbing often performed true attacks on the buzzard. The latter, however, generally paid no apparent attention to them. The mobbing rate, without regard to the corvid species, varied between the seasons ($\chi^2_{(6)} = 19.30$, $P < 0.01$). The attacks were continuous (more than one attack/10 sec) in spring, at intervals (less than one attack/10 sec) in autumn, and rare (less than one attack/60 sec) in winter. The season greatly affected both the number of attacking birds and the total duration of the interaction (Table 3). The maximum number of mobbing individuals was much higher in spring and summer in all corvid species ($H = 12.85$, $N = 317$, $P < 0.001$ in the hooded crow; $H = 9.93$, $N = 63$, $P < 0.05$ in the magpie; $H = 16.59$, $N = 50$, $P < 0.001$ in the jay). Corvids mobbed longer in spring and summer (jay and magpie). The frequency of interaction decreased with number of days post-release for hooded crow ($r = 0.22$, $N = 92$, $P < 0.05$) but not for the magpie and jay. Similarly, the frequency of vocalizations by the mobbing hooded crows was affected by the season ($\chi^2_{(6)} = 87.48$, $P < 0.001$). Vocalizations were almost continuous (more than one vocalization/5 sec) in spring, less frequent (less than one vocalization/5 sec) in winter, and virtually absent in autumn.

Several other bird species interacted with released buzzards, but these were too infrequent to allow statistical evaluation. Seventeen interactions occurred with common kestrels (*Falco tinnunculus*), mostly during spring near the kestrels' nests. A few interactions occurred with the marsh harrier (*Circus aeruginosus*) and hen harrier (*Circus cyaneus*) during autumn and winter in open habitats. Interactions with sparrowhawks (*Accipiter nisus*) occurred at the

Table 3. The mean (\pm SE) duration (minutes) of interactions and the mean (\pm SE) number of attacking birds in three corvid species in each season.

SEASON	HOODED CROW		MAGPIE		JAY	
	DURATION	NO. BIRDS	DURATION	NO. BIRDS	DURATION	NO. BIRDS
Spring	5.62 \pm 0.59	1.50 \pm 0.16	4.38 \pm 1.13	0.83 \pm 0.32	4.47 \pm 0.86	1.08 \pm 0.23
Summer	9.89 \pm 1.21	1.56 \pm 0.16	4.37 \pm 0.98	0.29 \pm 0.24	3.82 \pm 0.95	0.69 \pm 0.24
Autumn	9.42 \pm 1.74	0.91 \pm 0.13	1.88 \pm 0.31	0.06 \pm 0.04	1.05 \pm 0.21	0.05 \pm 0.05
Winter	14.54 \pm 3.22	0.84 \pm 0.18	1.85 \pm 0.35	0.00 \pm 0.00	2.70 \pm 0.30	0.00 \pm 0.00

end of spring. Finally, several non-corvid Passeriformes and two species of Columbidae interacted occasionally.

DISCUSSION

Many of the buzzards were able to survive for several weeks around the release site. Although varying in timing and direction, the abandonment of the release site was similar to what has been recorded for rehabilitated congeneric American species (Hamilton et al. 1988). However, we recorded a greater distance than reported for buzzards released in wooded habitat (Llewellyn and Brain 1983) suggesting that areas lacking large woods are likely not attractive for long-term occupation, possibly because of the lack of hiding places. The survival of buzzards for prolonged time in this study shows that release in areas heavily populated by humans is not very detrimental to the birds as was claimed by Hamilton et al. (1988).

On the other hand, lack of muscle tone just after release likely reduces the readiness to disperse from the release site (Servheen and English 1979). Low muscle tone is certainly caused by prolonged captivity that in turn is correlated with the frequency of flights and quick dispersal. Nevertheless, it is unlikely that it induces great vulnerability to the bird as claimed by Duke et al. (1981). Although repeated flights in training aviaries at the RRC were very important, they seemed to be inadequate for long distance flights soon after release. Nonetheless, good muscle tone and endurance appeared to be achieved in a very few days.

Similar to American species (Duke et al. 1981), the season that release occurred in clearly affected the time of dispersal and the type of flight. In fact, although the Italian population is basically non-migratory, the type of flights performed in spring and autumn (higher, longer, and frequent soaring) are

associated with a migratory behavior. Moreover, quick departure from the release site was recorded only during the migration period.

The frequency of hunting attempts by our released birds was high and possibly underestimated. Our data do not support the hypothesis by Hamilton et al. (1988) that in red-tailed hawks (*Buteo jamaicensis*) and broad-winged hawks (*Buteo lineatus*) unfamiliarity with the new area or captive feeding negatively affect hunting behavior. Even other parameters related to prey catching ability, attack glide (Wakeley 1978), and the prey attack angle (Janes 1985) were similar to those of congeneric wild birds.

Predatory proficiency of our birds likely improved with repetition. Prolonged captivity did not seem to be detrimental to hunting ability from perches, as previously suggested in laboratory conditions (Csermely et al. 1991). Such an ability is shown by the wide range of taxa taken as prey by our rehabilitated birds, a range very similar to the diet of wild Mediterranean populations (Lovari 1974, Manzi and Pellegrini 1989, Mañosa and Cordero 1992). The increased success of prey capture with days post-release was possibly connected to an increased knowledge of the environment. The increase in hunting attempts in migratory periods may have been due to increases in metabolism connected with migration. Retaliation to a wild buzzard attack was rare in the early post-release days but the frequency of interactions increased with time after release. Interactions, although frequent during reproductive and migration periods (Brown 1989), did not cause buzzards to leave the area which was opposite of the case for red-tailed hawks (Hamilton et al. 1988). Mobbing by corvids seemed to cause only the buzzard's abandonment of perches. This was true in spring and summer, when the corvids have greater parental motivation toward antipredatory behavior

(Röell 1982). The hooded crow, due to its large size and great sociality, is the species with the greatest ability to chase buzzards. However, antipredatory behavior by the corvids did not seem to have a very detrimental effect on buzzard releases.

In conclusion, released buzzards showed a ready ability to cope with the environment and to acclimate to the wild. Prey was captured quite easily even after prolonged captivity, although a certain level of training was evident. Moderate human presence around the release site did not appear detrimental. A greater source of interference likely came from mobbing corvids that sometimes forced buzzards to move from perches. From an applied point of view we can say that the rehabilitation technique was basically correct, because none of the buzzards showed evident behavioral modifications related to the captivity period.

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SHORT COMMUNICATIONS

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PARATHION POISONING OF MISSISSIPPI KITES IN OKLAHOMA

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KEY WORDS: *Ictinia mississippiensis*; *Mississippi kite*; *parathion*; *poisoning*.

Parathion (phosphorothioic acid O, O-diethyl O-[4-nitrophenyl] ester) is a broad spectrum organophosphorus insecticide, used on a variety of crops and occasionally for mosquito control, and is highly toxic to birds (Smith 1987). Intentional poisoning with parathion is reported to have killed more than 8000 red-winged blackbirds (*Agelaius phoeniceus*), common grackles (*Quiscalus quiscula*), brown-headed cowbirds (*Molothrus ater*) and European starlings (*Sturnus vulgaris*) in two separate instances (Stone et al. 1984). Use of parathion on wheat fields has resulted in the mortality of about 1600 Canada geese (*Branta canadensis*) and other waterfowl in one instance (White et al. 1982) and about 200 Canada geese in another (Flickinger et al. 1991). More than 200 laughing gulls (*Larus atricilla*) died near cotton fields treated with parathion (White et al. 1979). Secondary poisoning of raptors, resulting from the consumption of prey exposed to parathion, has been reported experimentally and in the field. Stone et al. (1984) found two dead red-tailed hawks (*Buteo jamaicensis*), a Cooper's hawk (*Accipiter cooperii*) and an American kestrel (*Falco sparverius*) that had fed on blackbirds killed by parathion. One of four American kestrels died after being fed cricket frogs (*Acris crepitans*) that had been exposed to 10 ppm parathion for 96 hr (Fleming et al. 1982). The Mississippi kite (*Ictinia mississippiensis*) is highly insectivorous (Brown and Amadon 1968) and is thus subject to secondary poisoning resulting from consumption of insects exposed to pesticides. I report here an instance of secondary parathion poisoning in wild Mississippi kites.

STUDY AREA AND METHODS

On 25 August 1988, two sick and 14 dead Mississippi kites were collected at the edge of a golf course near Altus in southwest Oklahoma. One owl, two rabbits, and several

ground squirrels, all of unidentified species, were also found dead in proximity to the kites but were not examined. Adjacent to the golf course were cotton fields recently sprayed with pesticides and, although inquiries were made, the specific compound(s) used remain unknown. There was no history of recent pesticide application to the golf course. Three of the dead kites were sent to the National Wildlife Health Research Center for necropsy. Brains from these three carcasses, and from one bird collected as a control by shooting, were tested for cholinesterase activity by the method of Ellman et al. (1961) as modified by Hill and Fleming (1982). Stomach contents were pooled from the three birds found dead and sent to the Patuxent Wildlife Research Center and analyzed by column extraction and gas chromatography for 24 organophosphorus compounds and six carbamates (Belisle and Swineford 1988, Patuxent Analytical Control Facility standard operating procedure 0-25.00). The lower limit of reportable residues was 0.1 ppm wet weight for organophosphorus compounds and 2.45–4.90 ppm wet weight for carbamates.

RESULTS AND DISCUSSION

Clinical signs exhibited by the two sick birds included frothy oral discharge, weakness, inability to stand, and stumbling gait—all compatible with exposure to an anticholinesterase agent (Grue et al. 1991). These birds recovered after being given ground beef and water. Examination of the three carcasses revealed that two were adult females and the third was a male of undetermined age. All three were in fair body condition with only traces of subcutaneous fat, had large amounts of unidentified insect remains in their stomachs, and no lesions suggestive of trauma or infectious disease. Brain cholinesterase activities in the three birds found dead were 1.0–1.1 $\mu\text{mol}/\text{min}/\text{g}$ (wet weight), compared with 9.2 $\mu\text{mol}/\text{min}/\text{g}$ (wet weight) for the control bird. These results suggested death was due to an anticholinesterase pesticide (Ludke et al. 1975) and incubation of the sample for 18 hr at 37°C resulted in no increase of brain cholinesterase activity, implicating an organophosphorus compound (Hill and Fleming 1982). Parathion (0.69 ppm wet weight) was the only pesticide found in detectable levels in the sample of pooled stomach contents, and its presence in the sample was confirmed by gas chromatography/mass spectroscopy.

The history of recent pesticide application to adjacent cotton fields, the proximity of sick Mississippi kites ex-

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hibiting clinical signs compatible with anticholinesterase poisoning, and laboratory findings in kites found dead point to parathion as the cause of mortality in this event. The presence of insect remains and parathion in the stomachs of these birds suggest they were secondarily poisoned after consuming insects exposed to parathion, probably applied to cotton fields adjacent to the golf course. This is the first documentation of Mississippi kites dying of anticholinesterase poisoning and parallels a case in south Texas where laughing gulls died after feeding on insects in cotton fields recently sprayed with parathion (White et al. 1979).

RESUMEN.—El 25 de agosto de 1988 se encontraron dos individuos enfermos de *Ictinia mississippiensis* y 14 individuos muertos, en el campo de golf Altus, Oklahoma. Las señales clínicas observadas sugirieron un envenenamiento por anticolinesterasa. Se diagnosticó un envenenamiento por "parathion," luego que la evaluación de laboratorio reveló inhibición de colinesterasa cerebral de un 88–89% y la presencia de "parathion" (0.69 ppm, peso húmedo), en el contenido estomacal. Cultivos de algodón adyacentes al campo de golf habían sido recientemente rociados con un (os) pesticida (s) desconocido (s). No hubo antecedentes recientes de aplicación de pesticidas al campo de golf. El contenido estomacal consistió en restos de insectos y es probable que los individuos de *I. mississippiensis* se hayan envenenado secundariamente, luego de consumir insectos expuestos a la aplicación de "parathion" en los campos de algodón.

[Traducción de Ivan Lazo]

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STATUS AND REPRODUCTION OF THE PEREGRINE FALCON AT A
COASTAL LAGOON IN BAJA CALIFORNIA SUR, MEXICO

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KEY WORDS: *peregrine falcon; nesting; Mexico; Baja California; Falco peregrinus.*

The peregrine falcon (*Falco peregrinus*) is considered an endangered species worldwide (King 1981). Its status is not well known in Mexico (Banks 1969, Fyfe et al. 1976). Peregrine distribution has been considered to be restricted to the north and northwest of Mexico (see Thelander 1978), with the largest numbers in the Gulf of California and the Baja California peninsula (Banks 1969, Porter et al. 1988). Banks (1969) estimated the Gulf of California and the Baja California peninsula peregrine populations to contain about 66 nests, 38 of them on the Pacific side. However, later reports show the population on the west coast of the peninsula to be very small, declining drastically, or even disappearing (Anderson 1976, Porter et al. 1978, 1988). This decline was apparently at least partly caused by high levels of organochlorine pesticides (Porter et al. 1978, 1988, Kiff 1988).

Since 1977, when only one peregrine nest site was known on the Pacific side of Baja California, little additional information has been obtained for the west coast (Porter et al. 1988). During 1993, we found several active nests in the Ojo de Liebre (Scammon's) Lagoon, a location without historical nesting records. Here, we report on the peregrine status at this location, and provide information on nesting chronology and reproductive success.

STUDY SITE AND METHODS

Ojo de Liebre Lagoon is located on the west coast of the middle Baja California peninsula, about 650 km south of the United States/Mexico border (Fig. 1). It is the largest of three lagoons (360 km²) that open to the Vizcaino Bay. Descriptions of the lagoon can be found in Lewis and Ebeling (1974) and Saunders and Saunders (1981).

To locate peregrine nests, we explored potential sites, such as man-made structures located on the lagoon by boat, and investigated the islets on foot. Each nest found was checked directly at least four times between the third week of March and the third week of June. A nest where eggs were laid was considered active; a nest where at least one young fledged was considered productive.

RESULTS AND DISCUSSION

We found three breeding peregrine pairs in the lagoon. Two nests were on top of metallic, 3-m high, channel markers in the water near the sand dunes on the coast. These towers were constructed after 1967 (J. Peralta pers. comm.). The third nest was on the ground, in a small

conical rocky cavity (40 × 60 × 120 cm), on a low islet. This islet was visited by coyotes (*Canis latrans*) which periodically eradicated the ground-nesting ospreys (*Pandion haliaetus*) there (Kenyon 1947, Jehl 1977, Henny and Anderson 1979, Castellanos 1983).

According to Banks (1969), no breeding peregrines were sighted at the Ojo de Liebre Lagoon. Since then, there have been no additional peregrine sightings or reported nests in this area (see Banks 1969, Porter et al. 1988, Wilbur 1987). However, there are several unpublished sightings of resident peregrines and nesting pairs in this area for 1977 (C. Henny and D. Anderson pers. comm.), 1984, and 1992 (F. Jaramillo and F. Heredia pers. comm.).

Nesting occurred between the first part of March, when the eggs were laid, to late June, when all the young had abandoned their nests or were able to fly. Laying seems to have occurred between February and March, which is consistent with previous reports of egg laying dates (Porter et al. 1988). Eggs apparently hatched between the last week of March and the third week of April. The young fledged between the second week of May and the third week of June.

The clutch size averaged 3.3 eggs. The occurrence of two sets of three eggs is consistent with Bancroft (1927) who explained that on the Baja California peninsula, three egg clutches are more frequently laid than clutches of four. An average of 3.0 nestlings and 2.6 fledglings was produced in each active nest; both values are greater than those reported (nestlings = 2.17, fledglings = 1.74) for the Gulf of California peregrines during 1976–1984 (Porter et al. 1988). There was no significant difference between the average number of fledglings produced on the Gulf of California and this study ($t = 1.76$, $df = 28$, $P > 0.05$).

Our exploration revealed a limited number of potential nesting sites such as cliffs or relatively secure man-made structures in the study area. Indeed, we believe that the observed peregrines represented the total number of resident breeding pairs in the Ojo de Liebre Lagoon. Two of the nests were located on towers constructed in the late 1960s and the third was in a site which had been visited by coyotes for several years, presumably preventing peregrine nesting. Thus, we believe that peregrine falcons have been nesting in the lagoon for no more than 20 yr.

Our data suggest that Ojo de Liebre Lagoon is an important peregrine breeding location in the middle west coast of Baja California. However, commercial fishing, tourism and channel markers maintenance activities are the primary threats to the peregrines in the area. The ground nest is accessible by walking visitors and fishermen who use the islet as a base. Nests on towers can be disturbed by fishermen operating around the towers or by the maintenance workers. Consequently, we believe that a special

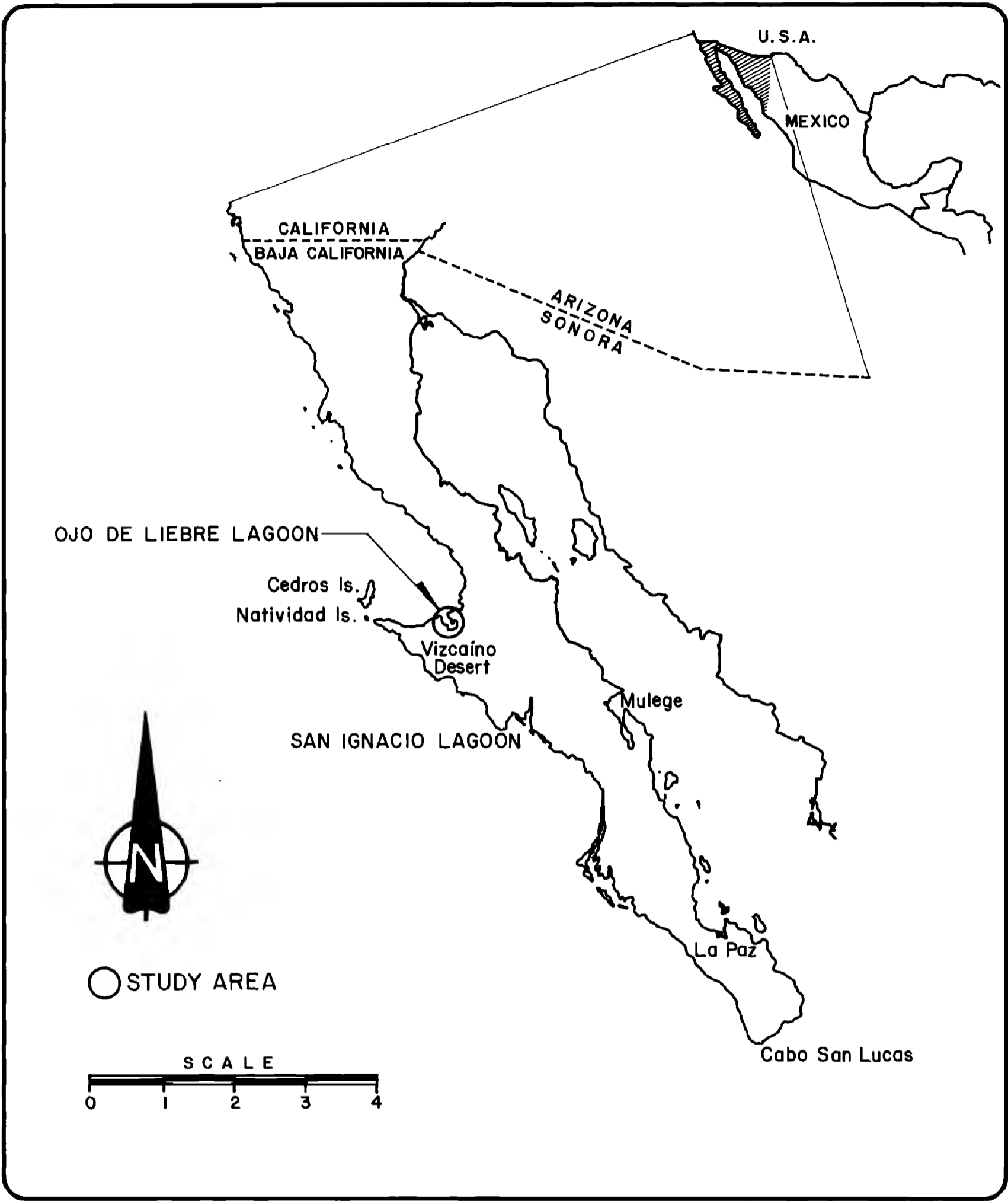


Figure 1. Location of the Laguna Ojo de Liebre (Scammon's Lagoon), Baja California Sur, Mexico.

effort needs to be made by government agencies to protect these nesting sites.

RESUMEN.—El halcón peregrino (*Falco peregrinus*) está considerado mundialmente en peligro y su estatus en México es poco conocido. En recientes reportes se considera a la población anidante en la costa del Pacífico de la península de Baja California desapareciendo o muy reducida en números. Durante 1993, nosotros encontramos tres parejas de peregrino en la laguna Ojo de Liebre, en la costa del Pacífico de la península, donde no había registros previos de anidamiento. Los nidos estaban ubicados uno directamente en el suelo y dos sobre torres de señalamiento marítimo dentro del agua. El anidamiento ocurrió entre la primera mitad de marzo y finales de junio. El número promedio de volantones producido por nido activo fue de 2.6. La principal fuente de amenaza para los peregrinos en el área de estudio es la perturbación humana. Recomendamos la protección efectiva de los sitios de anidamiento.

[Traducción Autor]

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SUCCESSFUL NESTING BY A PAIR OF BALD EAGLES AT AGES THREE AND FOUR

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KEY WORDS: *bald eagles; Kansas; nesting; plumage; sub-adult.*

Sexual maturity in the bald eagle (*Haliaeetus leucocephalus*) is commonly thought to occur after the bird attains a completely white head and tail, typically at age 4 yr (Clark and Wheeler 1987). Various factors probably influence initial reproductive attempts by individual eagles, so plumage is not always a reliable indicator of age or reproductive readiness (McCollough 1989). In 1993, a pair of bald eagles in subadult plumage nested in eastern Kansas. The nesting pair consisted of a 4-yr-old male and 3-yr-old female, and they successfully fledged one eaglet.

OBSERVATIONS

The nesting eagles were found at Hillsdale Reservoir in eastern Kansas, 40 km south of Kansas City. The pair occupied a nest in a large dead tree standing in water. They were first observed on the nest on 25 March 1993. Each bird wore a standard U.S. Fish and Wildlife Service aluminum band on one leg and a colored band on the opposite leg, and could thus be traced to its origin. The male parent was one of two males fledged in 1989 from a nest approximately 45 km northwest of the Hillsdale nest site. That was the first year bald eagles were documented nesting in Kansas since presettlement; Goss (1891) reported the bald eagle as resident in Kansas, with egg laying beginning in March, but provided no information on specific nests or locations. This eagle and its sibling fledged 16 July 1989, and were live trapped and banded 23 July. They left the area 9 August 1989, and neither was reported again until 1993.

The female hatched 16 January 1990 at the G.M. Sutton Avian Research Center in Bartlesville, Oklahoma, from an egg taken from a nest in Osceola County, Florida. She fledged 8 April from a hack tower at Eufaula Reservoir in eastcentral Oklahoma, approximately 345 km south of the Hillsdale nest, and was last seen in the area on 29 May 1990. She was not reported again until 1993. Radiotracking of previously hacked eagles by Sutton Center personnel indicate they sometimes initially disperse north as far as Canada.

We saw the parents exhibiting nestling feeding behavior on 7 and 8 April, but no eaglets were visible. No subse-

quent feeding behavior was observed over the next several days until 16 April, when one parent was observed feeding a small chick. We do not know if it was the same eaglet fed on 7 April.

The eagles were monitored periodically from April through June. Between 25 and 29 June the eaglet fledged, and was last seen at the reservoir on 17 July. High water levels in the reservoir during much of July and early August prevented adequate monitoring, so we do not know the actual departure date.

Reports of nesting by bald eagles in subadult plumage are rare. Hoxie (1910) reported successful reproduction by a pair in which both birds were in immature plumage, though the female was "beginning to show distinct traces of white in the tail." One hacked bird in Saskatchewan may have bred when only 3 yr old (Gerrard and Bortolotti 1988), and Hatcher (1991) reported successful nesting by a 3-yr-old male released in Tennessee. There are infrequent reports of birds in subadult plumage mating with an adult (Bent 1937, Stalmaster 1987). Sherrod et al. (1976) reported two different females in "eye-stripe" plumage that mated with males in adult plumage; one female laid eggs that did not hatch, but the other successfully produced two eaglets. "Eye-stripe" plumage, believed to "precede that of adult," is described as a basically white head with a brown eye stripe, and a white tail with brown banding or blotching (Sherrod et al. 1976). This plumage is analogous to subadult plumage E reported for bald eagles by Stalmaster (1987). We observed a pair at another reservoir in eastern Kansas in 1993, one of which showed plumage similar to subadult E. This pair appeared to be incubating, but for unknown reasons abandoned the nest prematurely.

Hancock (1973) reported that three of four pairs of adult bald eagles that eventually hatched eggs in captivity produced infertile eggs their first year of nesting, and no fertile eggs were produced until both parents were at least 5 yr old. Maestrelli and Wiemeyer (1975) speculated that the initial failure to reproduce by a captive 5-yr-old male and an 8-yr-old female was due to the male's physical immaturity. Captive bald eagles and golden eagles (*Aquila chrysaetos*) may attain adult plumage and begin reproducing later than wild birds, possibly due to diet and other factors (Jollie 1947, McCollough 1989).

Sandeman (1957) reported that subadult golden eagles sometimes occupy territories, form pairs, and construct nests, but generally produce no eggs. However, Teresa

(1980) reported an adult and a bird in subadult plumage which fledged two young. Teresa (1980) also stated that breeding by subadults in most eagle species occurs only under unusually favorable or unfavorable conditions. In Kansas, recent bald eagle nestings occurred after many decades of absence, and many suitable nesting sites are available. This may be creating an unusually favorable condition for population growth.

The bald eagle nest at Hillsdale Reservoir provided a unique opportunity to observe known-age birds in their first nesting attempt and to document plumage characteristics in wild birds of known age. The plumage of the male was virtually identical to subadult plumage E described by Stalmaster (1987). The plumage of the female closely matched Stalmaster's subadult plumage D. Had we not known this bird's age, we might have concluded that she was a 4-yr-old in delayed plumage. That conclusion would have been reinforced by her nesting success. The origin of the 4-yr-old male, a product of the first Kansas nest documented since presettlement, indicates the importance of ensuring breeding success by bald eagles initially colonizing a nesting area.

RESUMEN.—Una pareja de individuos de la especie *Haliaeetus leucocephalus* con plumaje subadulto establecieron un territorio de nidificación sobre una reserva al este de Kansas y en la primavera de 1993. Ambos individuos tenían anillos coloreados en sus patas, las que permitieron conocer sus edades y lugares de origen. El macho de cuatro años de edad, con plumaje de volanton en 1989, correspondiente al primer nido activo documentado en Kansas desde la precolonización. La hembra de tres años de edad, fue registrada en Oklahoma en 1990. La pareja empolló exitosamente un polleulo.

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TRAPS FOR CAPTURING TERRITORIAL OWLS

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A variety of techniques have been used to capture raptors (e.g., Berger and Hamerstrom 1962, Meng 1971, Fuller and Christenson 1976, Kenward et al. 1983, Bull 1987). Raptors are generally easier to capture during the breeding season when they can be caught in nest boxes (e.g., owls) or by placing traps at or near the nest. Outside the breeding season birds are more difficult to catch as their position at any one time is harder to predict. Exceptions to this are some North American owls which can be caught with comparative ease (Forsman 1983, Bull 1987).

Many owls defend territories, and can be caught by exploiting their behavior toward intruders. For example, the tawny owl (*Strix aluco*) vigorously defends territories throughout the year (Southern 1970), and can be caught using tape lures to attract birds to mist nets (Hirons 1976). Outside the breeding season tawny owls have also been caught while roosting in nest boxes (Baudvin and Dessolin 1992) or with the use of live prey as lures (Hardy 1992).

METHODS

During the winters of 1990–91 and 1991–92, three techniques were tested in an attempt to capture tawny owls in woods in Cambridgeshire, southeast England. Two of these traps rely on the fact that territorial owls defend their territory against intruders. The third uses prey to attract owls to the traps.

Mist Net and Tape Lure. Nets were set up inside known owl territories with a continuous tape of a hooting male placed underneath. These were watched for approximately 2 hr.

Large Modified Chardoneret Trap. This trap had three compartments; a large lower one containing a male tawny owl, and two upper ones in which owls were caught (Fig. 1). The lure owl was provided with suitable perches and cover from rain. The lid above each of the top compartments had a piece of stiff wire running down its center, which extended beyond its base and, when the trap was set, rested in a hole in the wooden trigger. The trigger was held against the wall of the trap by pressure from the lid wire. The perch was fixed to the wall of the trap and to the trigger. Pressure on the perch pulled the trigger down, which released the wire, allowing the lid to shut. The trap was held shut by two hooks at the end of the lid which snagged on the wire of the trap. The whole trap was constructed of 5 cm weldmesh. The trap was set with perches just above and in front of the open lids. It was placed in a territory at dusk, and checked at dawn.

Small Modified Chardoneret Traps. These traps operated as for the above trap, but this time the lower compartment was smaller (10 cm high) and contained prey species (house sparrows [*Passer domesticus*] or laboratory mice) as lures. The traps were similar in design to the falling-lid trap described by Kenward et al. (1983), based on an original design by Hamilton (Lundberg 1933). The lower compartment had a mesh size of 1 cm and contained food, water, and shelter for the lure species. Again, the traps were set with a perch just above and in front of the open lid. One or two of these traps were placed in each territory just before dusk and checked at dawn.

RESULTS AND DISCUSSION

None of the six capture attempts using nets was successful. Owls were twice seen to be attracted to the taped calls, but flew over or around the net. Due to the length of time required to set up and watch these nets, this method was dropped in favor of the traps. When the success rate of the two types of trap was compared, we found that the trap using the live owl (11 owls caught in 32 trap nights) was significantly more successful ($\chi^2 = 50.3$, $P < 0.001$) than the trap using live prey lures (5 owls caught in 253 trap nights). No more than one owl was ever caught per night per territory. All the owls were fitted with radio-transmitters and all were found to be territorial birds.

Some North American owls such as spotted owl (*Strix occidentalis*) and great grey owl (*Strix nebulosa*) appear relatively unafraid of humans and can be caught with apparent ease (Forsman 1983, Bull 1987). This is not the case with tawny owls which invariably fly when humans approach their roost sites. Outside the breeding season, tawny owls have previously been caught either in nest boxes (Baudvin and Dessolin 1992), with mist net and tape lures (Hirons 1976), or using live prey as lures (Hardy 1992). The use of nest boxes for roosting in the winter appears to depend on habitat type (Petty 1992), with birds less likely to use boxes where natural cover (e.g., coniferous trees) is abundant. In the present study owls rarely used boxes to roost in, preferring the cover of plants such as old man's beard (*Clematis vitalba*) or ivy (*Hedera helix*). The use of nets and tape lures to catch owls also proved ineffective and time consuming. The modified Chardoneret traps had an advantage in that they could be easily set and left overnight. Placing a live owl inside a bird's territory proved more effective at attracting owls to the trap than using prey species and this technique presents an effective method of capturing territorial owls, which compares favorably to other designs used to capture raptors outside the breeding season (see Kenward et al. 1983).

RESUMEN.—Rapaces, tales como *Strix aluco* son a menudo difíciles de capturar en la estación no reproductiva. Es-

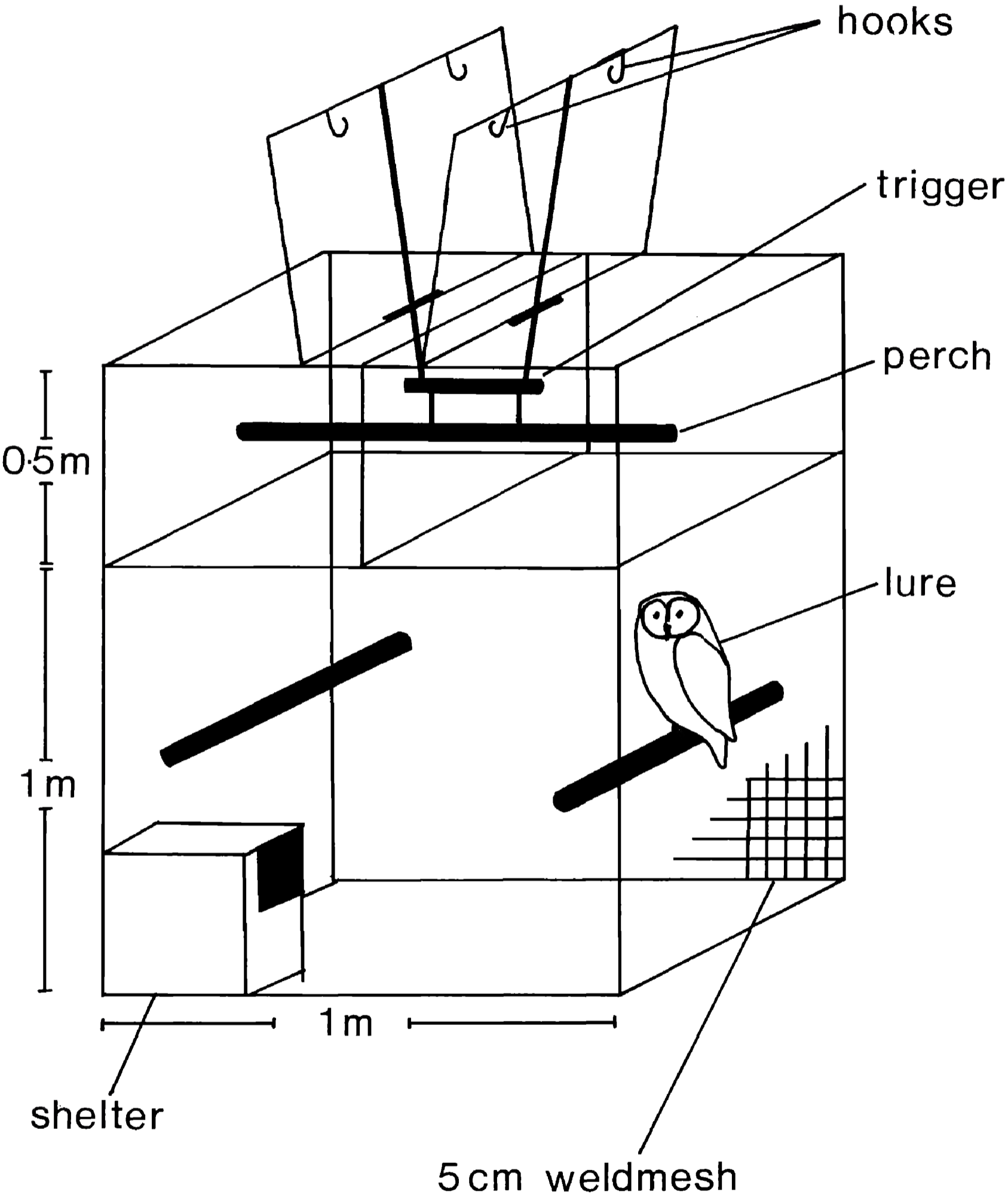


Figure 1. Large modified Chardoneret using a captive owl as a lure. Owls flew from an external perch into one of the top compartments, landing on the internal perch and releasing the trigger, thereby allowing the lid to close.

tudios previos describen la captura de aves mientras descansan en nidos caja, o usando redes de niebla y grabaciones señuelo. En este estudio, las aves fueron raramente encontradas descansando en nidos caja, de manera que otras tres técnicas fueron comparadas. Primero, redes de niebla fueron levantadas sobre una grabación señuelo y observadas durante dos horas. Los búhos fueron atraídos por la grabación pero volaron sobre o alrededor de la red. No hubo captura en seis intentos. Segundo, una Trampa Chardonnet modificada fue construida, se usó un macho vivo de *S. aluco* como señuelo. El búho cautivo se mantuvo en el compartimento inferior y las capturas se realizaban en el superior. El propio peso del búho aterrizando sobre una percha en el compartimento superior accionaba el mecanismo de cierre de la trampa. En la tercera técnica se utilizó una pequeña versión de la Trampa de Chardonnet modificada, aunque esta vez se utilizaron especies presa como señuelo y dispuestas en el fondo del compartimento. De las dos trampas, la primera (con búhos vivos) fue más efectiva (11 búhos en 32 noches-trampa) que la trampa que utilicé especies presas (cinco búhos en 253 noches-trampa). La diferencia fue significativa ($\chi^2 = 50.3$, $P < 0.001$). Esta trampa utiliza la conducta agresiva de búhos territoriales hacia intrusos y representa un efectivo método para capturar búhos territoriales.

[Traducción de Ivan Lazo]

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LETTERS

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FLUSH-HUNTING AND NEST ROBBING BY PEREGRINE FALCONS

Between 0610–1000 H on 25 November 1992, we observed the hunting behavior and interactions of an adult pair of peregrine falcons (*Falco peregrinus*) and their two fledged nestlings, in a steep-walled gorge on the lower Orange River, South Africa (28°S, 20°E). The young were still dependent on their parents for food, most of which was provided by the adult male.

At 0824 H the adult female was observed making an aerial transfer of food to the juvenile male. The prey appeared to be a half-grown rock pigeon (*Columba guinea*) squab. At 0827 H the adult female flew about 50 m to a rock pigeon nest, situated on a grass tussock on an open ledge about 20 m above the floor of the gorge, on the north wall. She removed a nestling, flew to a nearby perch and ate it. While raiding the nest, the peregrine was attacked by an adult rock pigeon. By 0833 H the adult female falcon had finished eating the squab, and returned to the now empty pigeon nest. She was again attacked by the pigeon, which actually landed on the peregrine's back and dislodged her from the ledge. The falcon fell backwards, turned and caught the pigeon, which managed to break free and fly down the gorge. The peregrine chased the pigeon for about 200 m before it found cover among some large boulders in the river bed. At 0835 H the peregrine female was seen to visit the pigeon nest for the third time. Again the pigeon defended its nest, but this time the falcon was able to grab and hold on to its attacker, and flew with the pigeon to a ledge 30 m upstream, where she killed it, plucked it and fed on it until 0947 H, when she flew out into the gorge and passed the remains of the pigeon to the juvenile male.

At 1115 H on 7 May 1993, ARJ watched a female peregrine at the same site land at a ledge where she was mobbed by two rock pigeons. The falcon tried to catch one of these pigeons and chased it down the gorge for about 200 m before flying back to perch on the cliff. At 1420 H the peregrine flew from a perch about 100 m upriver and landed at the same ledge, and had been perched there for about 5 min before she was again attacked by a pigeon which she caught, apparently very easily, without leaving the ledge. Although the hunting falcon was not seen to rob a pigeon nest at the ledge where this incident took place, this may have occurred sometime previously.

Large falcons, and especially peregrines, feed mostly on flying birds, which are caught in aerial chases. Observations of nest robbing by large falcons are infrequent in the literature (W. Fischer 1967, *Der Wanderfalk*, Ziemsen, Wittenburg; R.B. Treleaven 1981, *Br. Birds* 74:97; J.L.B. Albuquerque 1984, M.S. thesis, Brigham Young Univ., Provo, UT U.S.A.; A.J. van Zyl 1991, *Gabar* 6:68), although nestling birds (mostly of ground-nesting species) sometimes are identified from remains gathered at nesting and roosting sites (D.A. Ratcliffe 1980, *The peregrine falcon*, T. & A.D. Poyser, Calton, U.K.; R. Mearns 1983, *Bird Study* 30:81–90). In contrast, records of common kestrels (*F. tinnunculus*) robbing nests are quite frequent (e.g., D.W. Yalden 1980, *Bird Study* 27:235–238; F. van der Merwe 1986, *Promerops* 176:12–13; R.A. Pettifor 1990, *An. Behav.* 39:821–827; A.J. van Zyl 1991; S.K. Woolley 1992, *Br. Birds* 85:188). Kestrels are relatively slow, active-search hunters, which may account for the higher number of incidents of nest robbing reported for this species than for fast, pursuit-hunting falcons.

Given that a nest full of young birds is probably not a typical search image for these high-speed, aerial hunters, we are drawn to speculate on the conditions under which a peregrine might discover and utilize such a food source. African peregrines (*F. p. minor*) apparently “flush-hunt” on their nest cliffs relatively frequently (K. Hustler 1983, *Ostrich* 54:161–171; W. Tarboton 1984, *Raptor Res.* 18:131–136; ARJ pers. obs.). This hunting technique can involve the systematic searching of areas of the cliff, either from a perch or from the air, in order to locate, flush and then chase birds perched on the cliff. Falcons that flush-hunt regularly may be more likely to find nestling birds and prey on them than those that do not. We suspect that the frequency with which falcons flush-hunt may increase in situations where cliff-dwelling prey species are abundant in a pair's hunting range or, at the other extreme, where the frequency with which potential prey fly past cliff sites is low. The former conditions probably occur at the seabird colonies on the western Pacific islands, where flush-hunting by immature peregrines has also been reported (C.M. White cited in Tarboton 1984), and at temperate sea cliffs, where flush-hunting has been observed (A. Parker 1979, *Br. Birds* 72:104–114) and nest robbing at a gull colony has been recorded (R.B. Treleaven 1981, *Br. Birds* 74:97). The latter conditions may prevail at lower latitudes (see A.R. Jenkins 1991, *Gabar* 6:20–24), and flush-hunting has been observed in Argentina (C.M. White cited in Tarboton 1984), southern Brazil (Albuquerque 1984) and Mexico (D.V. Lanning *et al.* 1977, *Nat. Geog. Res.* 18:377–388), as well as in tropical Africa.

In the first incident described here, the adult male peregrine made at least 17 hunting attempts at flying prey during

the morning observation period, all within a 1-km stretch of the river gorge, and was successful on four (23.5%) occasions. The pair obviously was not subject to a low availability of flying prey. They were exploiting a prey base that was spatially concentrated in a short length of river gorge, and temporally concentrated by a common activity peak in the early morning. This prey base consisted of an abundance of aerial insectivores and other species found in close association with the river or the cliffs of the river gorge. Rock pigeons, and presumably their nests, were numerous in the gorge. We suspect that nest robbing is a fairly frequent occurrence in this pair.

We thank the Foundation for Research Development for financial support.—**Andrew R. Jenkins and Anthony J. van Zyl, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7700, South Africa.**

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CANNIBALISM OF A YOUNG BARN OWL (*Tyto alba*) BY ITS PARENTS

Cannibalism occurs fairly frequently in broods of many raptor species (C. Ingram 1959, *Auk* 76:218–226; C.H. Stinson 1979, *Evolution* 33:1219–1225; J.K. Terres 1980, *Aud. Soc. Encycl. North Am.*, Alfred A. Knopf, New York, NY U.S.A.). This behavior is adaptive in predatory species in times of food shortages, severe weather conditions, and disturbance at the nest, and contributes to their individual fitness. Cannibalism among barn owls (*Tyto alba*) has been reported (D.S. Bunn et al. 1981, *The barn owl*, Buteo Books, Vermillion, SD U.S.A.; B.A. Colvin 1984, Ph.D. diss., Bowling Green, OH U.S.A.; G.M. Lenton 1984, *Ibis* 126:551–575; Marti 1992, *Barn owl*, *Birds of North Am.*, *Acad. Nat. Sci., Phila.* 1:1–15), although it occurs less frequently than is popularly believed (D.S. Bunn et al. 1981). When food is abundant, nestling barn owls have been observed to share food with their younger siblings (C.D. Marti 1989 *Wilson Bull.* 101:132–134); however, when food is scarce, young barn owls have been observed to kill and consume their siblings, an act that could permit them to survive periods of severe food shortages (D.S. Bunn et al. 1981). The killing of an owlet by an adult and feeding it to the other young is the most unlikely of seven different cannibalism scenarios and has not been documented (D.S. Bunn et al. 1981). Reports of adult barn owls killing one of their own injured young and eating it or feeding it to their remaining young has also not previously been reported. Some circumstantial evidence exists to suggest that both of these scenarios can occur in North American barn owls (B.A. Colvin 1984).

In the process of studying a pair of nesting barn owls, I observed evidence of cannibalism in which one or both of the adults presumably killed and consumed one of their offspring during a period when food was becoming scarce.

I observed a pair of barn owls and their offspring on an abandoned herbicide manufacturing facility in Houston, Texas. I visited the site at 1–2 wk intervals from 10 April 1988 through 19 August 1989. The owls used a small brick structure (4.6 × 2.4 × 3.0 m) as a roosting/nesting site. A wooden box (0.3 × 1.2 × 0.3 m) above a small doorway, the only opening to the structure, served as a nest box. On 23 October 1988, a clutch of seven eggs was found in the nest. This was the second of three clutches produced by the owls during this 16-mo period. By 30 October, the first two eggs had hatched and by 12 November, a third egg had hatched and one egg remained in the nest; the other three eggs were missing. The remaining egg never hatched and disappeared within a week. The three owlets were last observed in the nest together on 17 December. On 24 December, both parents were seen at the roost and there were only two young still in the nest. The oldest owlet (57–59 d) was found dead on the floor and I observed the adult male sitting next to it. The owlet appeared to have been dead for about 1–2 d. Its body cavity had been ripped open, and it had been almost completely eaten. Only the wings, feet, skull, and stripped skeleton remained. It was not decapitated as is usually done with live prey and cannibalized young (D.S. Bunn et al. 1981) and its feathers were not scattered around the roost (K.L. Hamilton 1980, *Texas J. Sci.* 32:175). A necropsy on the dead owlet revealed a broken right humerus. I suspect that this occurred during practice flying within the small enclosed area, but may have been a result of falling out of the nest to the floor (about 2.6 m).

The barn owl roost and nest box were inaccessible to the few potential mammalian predators at the site and other avian predation was highly unlikely. In addition, the condition of the owlet's carcass strongly suggested that it had been eaten by the owls and not by another predator.

The hunger of either the parents or the remaining owlets, combined with the colder than normal temperatures at the time, probably led to this cannibalism. Pellet analyses indicated that prey were becoming scarce as winter progressed into 1989, and many birds and insects were found in the diet (unpubl. data).

Feeding behaviors such as cannibalism of healthy or injured young can be important in predatory species such as

barn owls during times of food shortage. However, this behavior usually is difficult to witness. More observations at raptor nest sites are needed to document the fate of nestlings that mysteriously disappear from their nests and to determine how frequent this behavior is and under what circumstances it occurs.

I thank W. McClure for field assistance with the ongoing barn owl study at this site, and J. Shaw, B. Colvin, J. Marks, and two anonymous reviewers for valuable comments on an earlier version of the manuscript.—**Steven R. Sheffield, Department of Zoology, Oklahoma State University, Stillwater, OK 74078 U.S.A.**

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OSPREYS (*Pandion haliaetus*) SCAVENGING FISH ON ICE

The diet and foraging behavior of ospreys (*Pandion haliaetus*) have been studied extensively in North America (A.C. Bent 1937, *U.S. Nat. Mus. Bull.* 167:352–379; T.C. Dunstan 1974, *Wilson Bull.* 86:74–76; J.E. Swenson 1978, *J. Wildl. Manage.* 42:87–90; A. Poole 1989, *Ospreys*, Cambridge Univ. Press, Cambridge, U.K.; S.P. Fleming et al. 1992, *Auk* 109:649–654), and other parts of the world (Y.A. Prevost 1982, Ph.D. thesis, Univ. Edinburgh, Scotland; S. Cramp and K.E.L. Simmons 1980, *The birds of the western Palearctic*, Vol. 2, Oxford Univ. Press, Oxford, U.K.). Live fish, caught by plunging into shallow water, comprised over 99% of the diet in each osprey population studied thus far (Poole 1989). In this paper we provide details of ospreys scavenging dead and dying fish, caught by fishermen, from the ice surface during the first week of nest site occupation in Canada.

Between 1 April and 6 April 1993, two ospreys were noted on artificial nest platforms in the Honey Harbour area of Georgian Bay, Lake Huron (44°51'N, 79°49'W). Ice cover was complete during this period on all water bodies within at least 8 km of these nest sites, and the main melt did not occur until the second week of April. In 1991 and 1992 the first ospreys were noted in this area on 7–8 April, and some of these birds flew up to 12 km to reach open-water fishing areas.

On at least three separate occasions in the 1–6 April period in 1993, the two ospreys were seen by one of us (EC) soaring and hovering above ice-fishing holes in a small bay 2 km from the nest sites. Fishermen were catching large numbers of black crappie (*Pomoxis nigromaculatus*) at this time, and usually left 15–30 cm fish on the surface of the ice. Since many different ice holes were fished by up to 50 people on some days, dead and dying black crappies were sometimes left unattended beside ice holes for up to 30 min. On several occasions both ospreys swooped down to the ice surface about 100 m from the nearest fishermen, and each flew off with a black crappie.

Ospreys have been noted previously to pick up dead or dying fish from the water surface or from shoreline rocks (Bent 1937, Dunstan 1974), but these appear to be the only published accounts of such behavior. We know of no other accounts of ospreys taking fish from the ice surface, but elsewhere in Lake Huron, fledgling ospreys occasionally take fish scraps thrown to them by fishermen (W. Davis pers. comm.). Ospreys regularly use large fish carcasses for nesting material (Bent 1937, Poole 1989), and we have noted this behavior in the Great Lakes. We have also recorded a male osprey picking up and eating a dead largemouth bass (*Micropterus salmoides*) floating at the water surface in Georgian Bay.

Ospreys arriving back at nest sites in northern parts of North America are often confronted with extensive ice coverage of foraging areas during the pre-laying period. These observations of freshly caught fish taken at ice-fishing holes reflect the osprey's adaptability in foraging techniques, and its remarkable tolerance of human presence.

The studies of osprey in the Great Lakes basin were funded by the Canadian Wildlife Service–Ontario Region, Environment Canada's Great Lakes Action Plan, and the Ontario Ministry of Natural Resources. We are also grateful to various colleagues at the Canada Centre for Inland Waters for logistical assistance.—**Peter J. Ewins, Canadian Wildlife Service, Environment Canada, Canada Centre for Inland Waters, P.O. Box 5050, Burlington, Ontario, L7R 4A6 Canada, and Elmer Cousineau, Brandy's Island, Honey Harbour, Ontario P0E 1E0, Canada.**

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UNUSUAL PARENTAL BEHAVIORS BY MALE NORTHERN GOSHAWKS

The parental role of male raptors during nesting is typically limited to providing food for their mates and young. It is uncommon for male raptors to participate directly in brood rearing, such as brooding or feeding nestlings (L.

Brown 1976, *Birds of prey: their biology and ecology*, A&W Publ. Inc., New York, NY U.S.A.; I. Newton 1979, *Population ecology of raptors*, Buteo Books, Vermillion, SD U.S.A.), though it has been documented for some species (L. Brown and D. Amadon 1968, *Eagles, hawks and falcons of the world*, McGraw-Hill Book Co., New York, NY U.S.A.). The aggressiveness of hungry and physically larger female nestlings may make adult male raptors reluctant to provide care (I. Newton 1978, *J. Zool.* 184:465–487; 1979). This may be especially true among accipiters, a genus possessing strong reversed sexual size dimorphism. P.A. Johnsgard (1990, *Hawks, eagles, and falcons of North America*, Smithsonian Inst. Press, Washington, DC U.S.A.) postulated that male accipiters never feed their young, but there are conflicting reports. For example, when female sparrowhawks (*Accipiter nisus*) are killed or are absent from the nest, the males will deliver food to the nestlings but will not feed them (D.A. Bannerman 1956, *The birds of the British Isles*, Vol. 5, Oliver & Boyd, Edinburgh & London U.K.; Newton 1979). N.F.R. Snyder (pers. comm.), however, observed a male Cooper's hawk (*A. cooperii*) that brooded and fed nestlings after the female had been killed. R.S. Palmer (1988, *Handbook of North American birds*, Vol. 4, Yale Univ. Press, New Haven, CT U.S.A.) reported that female northern goshawks (*A. gentilis*) will not allow males to remain in the nest area after the nestlings are a few days old. Conversely, Bannerman (1956) suggested that male northern goshawks will feed their nestlings but did not provide any supporting evidence.

Here we describe one observation of a male goshawk feeding nestlings and another of a male goshawk brooding nestlings in northern Arizona during the breeding seasons of 1990 and 1991. To our knowledge this is the first documentation of male goshawks providing direct parental care to nestlings while the female was present during all or part of the interaction. The study area and methods are described in C.W. Boal (1993, M.S. thesis, Univ. Arizona, Tucson, AZ U.S.A.).

On 13 July, 1990, at 0735 H, an adult male goshawk delivered a golden-mantled ground squirrel (*Spermophilus lateralis*) to a nest under observation. The nest contained two 30–34-d-old unattended nestlings. The male goshawk stood on the nest rim for a few moments, then fed the nestlings for 8 min. He stopped feeding the nestlings and flew out of view when the female goshawk approached the nest and gave "dismissal" vocalizations (J.H. Schnell 1958, *Condor* 60:377–403) at 0743 H. We detected no differences between the behavior of the male and female goshawks in feeding the nestlings or in the nestlings' responses to being fed by the male or female parent. Neither adult bird was banded, but identification of the sexes was possible by size comparison, plumage characteristics, and the behavior and vocalizations when interacting.

The second observation occurred at a nest where the adult female goshawk was banded but the adult male was not. On 22 June, 1991, the male brought a tassel-eared squirrel (*Sciurus aberti*) to a perch approximately 40 m from the nest tree at 1129 H. The female took the squirrel from the male, brought it to the nest, and began feeding the two 15–17-d-old nestlings. At 1225 H the male goshawk perched in a tree 15 m from the nest tree and made "cluck" vocalizations (Schnell 1958). The female goshawk immediately flew from the nest with the squirrel and began giving "dismissal" vocalizations from an unseen location in the nest stand.

The male goshawk flew to the nest at 1228 H. He walked about the nest and then assumed a brooding position, though he was unable to completely cover the nestlings. The nestlings allowed the male to brood them without displaying any indication of alarm. The female goshawk stopped vocalizing at 1245 H but remained out of view. The male continued to brood the nestlings until 1335 H, at which time he stood, stretched, and flew from the nest.

Nest defense is not the primary role of male goshawks during brood-rearing (Schnell 1958), thus a non-aggressive response to intruders would be expected in contrast to the vocal and aggressive nest defense behavior of female goshawks (Schnell 1958). To observe the males' response to human intruders while brooding, nest observations continued while two field assistants searched the nest area for prey remains and castings between 1300 and 1320 H. Expected behavior of an adult female goshawk at this stage of the nesting cycle would be to leave the nest, perch in a nearby tree while vocalizing, and making low attacking flights at the intruders. The male goshawk, however, showed little concern over the intrusions and remained in a brooding position, even closing both of his eyes for short intervals.

These two incidents were observed during 1539 hr of nest observations. Participation in the feeding and brooding of nestlings by male goshawks is apparently uncommon. However, this report documents that male goshawks can and occasionally do provide direct care to their nestlings.

These observations were made during a study funded by a cost-share agreement between the Southwestern Region of the USDA Forest Service and the University of Arizona. Kaibab Forest Products, the Arizona Wildlife Federation, and the Arizona Falconers Association also provided funding. We thank T.S. Estabrook, D.N. Gossett, and two anonymous reviewers for providing helpful comments and suggestions on an earlier draft of this manuscript.—**Clint W. Boal**, School of Renewable Natural Resources, University of Arizona, Tucson, AZ 85721 U.S.A.; **Erin L. Bibles**, USDA Forest Service, Safford Ranger District, Safford AZ 85548 U.S.A.; **Raymond E. Brown**, RR1 Box 445, Appleton, ME 04862 U.S.A.

BALD EAGLE ATTACKS ADULT OSPREY

Kleptoparasitism and agonistic interactions between bald eagles (*Haliaeetus leucocephalus*) and ospreys (*Pandion haliaetus*) are well documented (A.C. Bent 1937, U.S. Natl. Mus. Bull. 167; J.C. Ogden 1975, *Wilson Bull.* 87:496–505; J.M. Gerard et al. 1986, *Blue Jay* 34:240–246; Y. Prévost 1979, *Auk* 96:413–414). The details of only one attack by a bald eagle on an osprey have been documented, in this case a nestling which had just received a fish from one of its parents (S.P. Flemming and R.P. Bancroft 1990, *J. Raptor Res.* 24:26–29). The observers were unable to determine the fate of the nestling. Here, we describe an attack that resulted in the death of an adult osprey and we discuss possible reasons for the attack.

The observation was made at a distance of 200 m at a 300 ha lake in northeastern Nova Scotia within 15 km of where the only other described attack (S.P. Flemming and R.P. Bancroft 1990, *J. Raptor Res.* 24:26–29) occurred. At 0615 H on 4 May 1993, a mature bald eagle was seen pursuing a male osprey. The tail and approximately 7 cm of the body of a 12 cm-long white perch (*Morone americana*) could be seen protruding from the osprey's mouth. The osprey flew in an erratic trajectory at heights from 3–12 m above the lake surface in an apparent attempt to evade the eagle. A second eagle joined the chase from where it had been perched in a tree along the shoreline. Both eagles closed to within a few m of the osprey and after about 45 s one of the eagles grabbed the osprey with its talons. Both birds immediately fell to the water at which point the second eagle departed. The osprey ceased struggling within 30 sec of hitting the water and the eagle immediately began using its wings to paddle to the shore 125 m away, pulling the osprey behind it. The eagle began to pluck the osprey as soon as it reached the shore. It then dragged the osprey to higher ground, about 3 m away, and remained there for 45 min while eating it.

We retrieved the remains of the osprey after the eagle had departed. Except for parts of the digestive tract, the viscera had been eaten, along with the entire breast musculature and that of one wing and both legs. The head of the osprey was intact and it still had the perch protruding from its mouth. The crop and pharynx were engorged with a mass (approx. 0.25 kg) of tissue of fish that could not be identified. This tissue was in an advanced stage of digestion, apparently the osprey had been attempting to regurgitate it. The completely undigested white perch was lodged in the buccal cavity in a way that suggested the osprey had been trying to regurgitate it also. It appeared that regurgitating the fish would have been difficult for the flying bird because of the size and shape of the fish and the way the erect dorsal fin was protruding into the palate of the osprey.

The only other attack of a bald eagle on an osprey (S.P. Flemming and R.P. Bancroft 1990, *J. Raptor Res.* 24:26–29) apparently began as kleptoparasitism, a common occurrence, but the eagle was opportunistic in attacking the osprey. Kleptoparasitism can potentially lead to predation, although this has not been documented in birds (H.J. Brockmann and C.J. Barnard 1979, *Anim. Behav.* 28:487–514). It is probable that the attack described here was also a case of intended kleptoparasitism which led to predation; there was no evidence that the perch had been touched by the eagle. A possible reason for the eagle's attack is that it somehow recognized that the osprey was in distress and therefore vulnerable to predation.

We thank the St. Francis Xavier University Council for Research for supporting research on the social behavior of ospreys.—**J. MacDonald, Department of Physical Education and N.R. Seymour, Department of Biology, St. Francis Xavier University, Antigonish, Nova Scotia B2G 1C0 Canada.**

DISSERTATION ABSTRACT

REGULATION OF BALD EAGLE (*Haliaeetus leucocephalus*) PRODUCTIVITY IN THE GREAT LAKES BASIN: AN ECOLOGICAL AND TOXICOLOGICAL APPROACH

The bald eagle population, within and adjacent to the Great Lakes Basin, constitutes the greatest single population within the contiguous United States. Bald eagles were largely extirpated from the Great Lakes by the mid-1960s, due to the effects of DDE. Eagles began to repopulate and raise young again along the shores of the Great Lakes, with the exception of Lake Ontario, by the 1980s.

The studies reported here focused on factors limiting bald eagle populations. Ecological factors investigated included food habits, nest tree use, winter habitat use, and the identification of potential nesting habitat. Bald eagles primarily foraged on fish (suckers, bullheads, northern pike, carp, and freshwater drum). Eagle nests were built primarily in white pines, but in cottonwoods near Lake Erie. Potential nesting habitat exists along the shorelines of all Great Lakes, primarily along Lakes Huron and Superior. Habitat availability, however, may limit the Lake Erie subpopulation, which has little unoccupied habitat and great density of nesting eagles.

Toxicological aspects investigated included monitoring concentrations of PCBs and p,p'-DDE in plasma, mercury and selenium in feathers. Hematological biomarkers were used to assess health of eaglets. Bill deformities in nestlings were also investigated. Concentrations of p,p'-DDE or PCBs, but not mercury or selenium, were significantly, and inversely correlated with regional reproductive productivity and success rates. Lesser reproductive productivity in some lesser contaminated areas are believed to be related to greater nesting density.

Reproductive productivity of bald eagles within this population is primarily regulated by concentrations of organochlorine compounds along the shorelines of the Great Lakes, and density dependant factors in the interior, relatively uncontaminated areas. The continuing recovery of this population will depend on maintaining greater productivity in interior areas to compensate for lesser fecundity and greater adult mortality along the shorelines of the Great Lakes.—**William Wesley Bowerman IV. 1993. Ph.D. dissertation, Department of Fisheries and Wildlife, Institute for Environmental Toxicology, Ecology and Evolutionary Biology Program, Michigan State University, East Lansing, MI 48824 U.S.A. Present address: Department of Animal Science, Michigan State University, East Lansing, MI 48824 U.S.A.**

DISSERTATION ABSTRACT

FACULTATIVE MANIPULATION OF HATCHING ASYNCHRONY IN THE AMERICAN KESTREL (*Falco sparverius*)

The consequences of hatching asynchrony for nestling birds have been well studied, but the adaptive significance of hatching patterns is the subject of considerable controversy. My questions centered around the role of food in determining costs and benefits of asynchrony at different stages in the breeding cycle and in particular, whether American kestrels might practice individual optimization of hatching spans. I conducted experiments in both the pre-laying and brood-rearing stages and in the process, tested four hypotheses: 1) brood reduction, 2) sibling rivalry, 3) peak load, and 4) energetic constraints during laying.

I explored the costs and benefits of brood reduction from a theoretical perspective. I developed a model of facultative manipulation (individual optimization) of hatching based on the brood reduction hypothesis and the assumption that hatching patterns have different fitness payoffs in good and bad food years. When food resources during the nestling period were partly predictable from those during the pre-laying period, facultative manipulation of hatching seemed advantageous in many types of environments. Correlation analysis showed that small mammal numbers in summer were sometimes, but not always, predictable from those in spring.

Next, I examined the costs and benefits of asynchrony during the brood-rearing period. I measured growth and mortality of nestlings within four treatment groups (asynchronous, synchronous, food-supplemented, unsupplemented)

to test the brood reduction hypothesis. Fledging success did not differ between synchronous and asynchronous broods when food was poor, but consistent with the brood reduction hypothesis, nestlings died at a younger age in asynchronous broods. Asynchronous young did better in terms of growth when food was scarce but when food was more abundant, youngest nestlings in asynchronous broods still died despite apparently adequate food for the brood. Overall, the patterns of growth and mortality supported the brood reduction hypothesis for kestrels when food was limited, but not when it was abundant.

To test whether asynchrony affected parental effort, I measured provisioning rates to synchronous and asynchronous broods. Parents of synchronous broods made up to 31% more visits to the nest than parents of asynchronous broods by the time nestlings were 25-d old. Despite the higher provisioning rate, nestlings from synchronous broods weighed less at fledging. Patterns of food provisioning were consistent with the sibling rivalry hypothesis but not with the peak load hypothesis. Finally, I examined the proximate effect of food on asynchrony during the pre-laying period. In good food years, the hatching spans of clutches were more synchronous than in poor years. Similarly, parents on good territories and females in good physical condition had synchronous broods compared to parents with less food. Kestrels that were supplemented in the pre-laying period laid larger eggs and hatched those eggs more synchronously. These results were consistent with the hypothesis of facultative manipulation of hatching spans but not with the energetic constraint hypothesis. Kestrels seemed to "choose" an appropriate degree of asynchrony based on food levels in the pre-laying period.—**Karen L. Wiebe. 1993. Ph.D. dissertation, Department of Biology, University of Saskatchewan, Saskatoon SK, Canada S7N 0W0. Present address: Department of Forest Sciences, 2357 Main Mall, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.**

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1994 ANNUAL MEETING

The Raptor Research Foundation, Inc. 1994 annual meeting will be held on 3–6 November at the Little America Hotel in Flagstaff, Arizona. Details about the meeting and a call for papers will be mailed to Foundation members in the summer, and can be obtained from Dan Varland, Scientific Program Chairperson, ITT Rayonier, Inc., Northwest Forest Resources, P.O. Box 200, Hoquiam, WA 98550, (telephone 206 533-7000), and Patricia Hall, Local Chairperson, 436 E. David Drive, Flagstaff, AZ 86011 U.S.A. (telephone 602 774-0041). For information about the associated symposia contact: Susi MacVean (northern goshawk), Arizona Game and Fish Department, 2222 W. Greenway Road, Phoenix, AZ 85023 U.S.A. (telephone 602 789-3581); Joseph Ganey (Mexican spotted owl), USDA Forest Service, Rocky Mountain Forest and Range Research Station, 2500 Pine Knoll Drive, Flagstaff, AZ 86011 U.S.A. (telephone 602 556-2156); Michael Fry (Swainson's hawk), Department of Avian Science, University of California, Davis, CA 95616 U.S.A. (telephone 916 752-1201).

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- The **Dean Amadon Award** recognizes an individual who has made significant contributions in the field of systematics or distribution of raptors. Contact: **Dr. Clayton White, 161 WIDB, Department of Zoology, Brigham Young University, Provo, UT 84602 U.S.A.** Deadline August 15.
- The **Tom Cade Award** recognizes an individual who has made significant advances in the area of captive propagation and reintroduction of raptors. Contact: **Dr. Brian Walton, Predatory Bird Research Group, Lower Quarry, University of California, Santa Cruz, CA 95064 U.S.A.** Deadline: August 15.
- The **Fran and Frederick Hamerstrom Award** recognizes an individual who has contributed significantly to the understanding of raptor ecology and natural history. Contact: **Dr. David E. Andersen, Department of Fisheries and Wildlife, 200 Hodson Hall, 1980 Folwell Avenue, University of Minnesota, St. Paul, MN 55108 U.S.A.** Deadline: August 15.

Recognition and Travel Assistance

- The **James R. Koplin Travel Award** is given to a student who is the senior author of the paper to be presented at the meeting for which travel funds are requested. Contact: **Dr. Petra Wood, West Virginia Cooperative Fish and Wildlife Research Unit, P.O. Box 6125, Percival Hall, Room 333, Morgantown, WV 26506-6125 U.S.A.** Deadline: Deadline established for conference paper abstracts.
- The **William C. Andersen Memorial Award** is given to the student who presents the best paper at the annual Raptor Research Foundation Meeting. Contact: **Ms. Laurie Goodrich, Hawk Mountain Sanctuary, Rural Route 2, Box 191, Kempton, PA 19529-9449 U.S.A.** Deadline: Deadline established for meeting paper abstracts.

Grants²

- The **Stephen R. Tully Memorial Grant** for \$500 is given to support research, management and conservation of raptors, especially to students and amateurs with limited access to alternative funding. Contact: **Alan Jenkins, George Miksch Sutton Avian Research Center, Inc., P.O. Box 2007, Bartlesville, OK 74005-2007 U.S.A.** Deadline: September 10.
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¹ Nominations should include: 1) the name, title and address of both nominee and nominator, 2) the names of three persons qualified to evaluate the nominee's scientific contribution, 3) a brief (one page) summary of the scientific contribution of the nominee.

² Send 5 copies of a proposal (≤5 pages) describing the applicant's background, study goals and methods, anticipated budget, and other funding.